Defining the Predator Landscape of Northeastern British Columbia

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Abstract

My research represents the predator (wolves, *Canis lupus*, and grizzly bears, *Ursus arctos*) component of a collaborative endeavor to examine processes that structure the multi-predator multi-prey system of the undisturbed Besa-Prophet watershed in the northern Rocky Mountains, northeastern British Columbia, Canada. It incorporated seasonal movements and range use, resource selection models, and isotopic assessments of prey selection to better understand predator use of the landscape. Mean annual range sizes of five wolf packs and 13 female grizzly bears were 801±118 km^2 and 334±33km^2, respectively. Sizes of annual, denning and late-summer ranges of wolves were proportional to the extent of conifer habitat and related to pack size, whereas winter and late-winter ranges appeared to be a function of movement rates. Most wolf packs used lower elevations during the winter and late-winter seasons and higher elevations during denning, late summer, and fall. Wolves showed highest selection for areas of high habitat diversity. They tended to select shrub habitats year-round and burned habitat classes seasonally, and avoided conifer classes. For grizzly bears, sizes of annual home ranges were inversely related to the extent of available *Elymus*-dominated burns; and seasonal ranges and movement rates were a function of family status. Grizzly bears generally were found at higher elevations during spring, lower elevations during fall, and across elevational gradients during summer. Shrub and burned habitat classes were important to grizzly bears year-round, and conifer classes were consistently avoided. Habitat selection by grizzly bears was best predicted from habitat class, elevation, aspect, and vegetation diversity. Moose (*Alces alces*) and elk (*Cervus elaphus*) dominated the diets of wolves. Both male and female grizzly bears increased meat intake (primarily elk) in the fall and males

consumed more meat than females throughout the year. Estimates of prey proportions in the diets of wolves and grizzly bears were highly sensitive to the fractionation values incorporated in isotope models. This research provides a comprehensive analysis of habitat selection and habitat use by wolves and grizzly bears that contributes to the long-term management and persistence of these populations.

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Chapter 1: Introduction

Background

Many mammalian carnivores are sensitive to landscape change because of their low population density, limited dispersal ability across open or developed habitats, and other traits that lower ecological resilience (Weaver et al. 1996). Defining animal distribution and movements across the landscape is vital to developing sound land-use management plans. Equally important, however, is quantifying mechanisms that drive these broad-scale patterns. Landscape ecologists have concentrated on quantifying landscape patterns, and identifying factors responsible for the development of the patterns (Riitters et al. 1997). It has proven more difficult to link those patterns to interpretations or assessments of ecological processes (Wiens et al. 1993), in part because wildlife species interact with the landscape at various scales (Johnson 1980). Wildlife habitat has typically been evaluated through measures of within-site habitat quality, but habitat availability and suitability vary spatially across the landscape (or region). Accounting for this variability and how animals respond to it is important to habitat assessments for a suite of species (Riitters et al. 1997).

Animal movements, dispersal, and habitat selection are the primary determinants of the spatial distribution of populations in heterogeneous landscapes. Ultimately, the types of information available to an animal as it moves across the landscape, and how this translates into patch or habitat choice, drive population dynamics (Kareiva 1990; Danielson 1991; Pulliam et al. 1992; Wiens et al. 1993). Many existing models for carnivores in the Rocky Mountains are conceptual models that have evolved out of a site-level planning paradigm (Carroll et al. 2001a) (e.g., habitat suitability index (HSI) modeling based on terrestrial ecosystem mapping (TEM)). In contrast, empirical models that make use of extensive data

sets allow the incorporation of variation in habitat relations across a landscape and exploration of the fit between alternate models and the data (Carroll et al. 2001b; Nielsen et al. 2003). Although the results of empirical modeling may not be easy to interpret mechanistically, they can provide initial estimates of population distribution through the use of resource selection functions and other techniques (Manly et al. 1993; Boyce and McDonald 1999), and can be useful in quantifying relative habitat values.

Goals and Objectives

The Besa-Prophet multi-predator multi-prey system in the Muskwa-Kechika Management Area of northeastern British Columbia (BC) is currently a relatively undisturbed ecosystem for which detailed data describing the interactions among focal species can be used towards future conservation and management planning for resource extraction. My study makes a significant contribution towards providing a better understanding of this predator-prey system that will enable developing a framework from which to monitor subsequent impacts. The research uses current techniques and recent technologies, including global positioning systems (GPS), geographic information systems (GIS), remote-sensing satellite imagery, stable-isotope analyses, and resource selection functions to quantify the predator landscape in the Besa-Prophet system. The overall goals of my study were to monitor movements of wolves and grizzly bears and identify seasonal habitats, to develop selection models that describe their use of the landscape, and to quantify seasonal prey selection. With these goals in mind, I structured my thesis around three objectives.

Objective 1. To identify factors that contribute to annual and seasonal variation in home-range sizes and movement rates of predators in the Besa-Prophet study area.

Numerous studies have established that range size and movement patterns of wolves are related to prey availability (density) and distribution, concluding that smaller ranges and increased tolerance to intruders/transients/immigrants result from high prey density and/or diversity, and degree of kinship (Fuller 1989; Cook et al. 1999). Average wolf-pack territory sizes vary 14-fold among areas across North America (Fuller et al. 2003). Average territory size and the average area per wolf vary most directly with food resources or prey abundance, as well as with prey type and the mean annual rate of population change (Fuller et al. 2003). For grizzly bears, movement patterns among and within populations are influenced by key food items, reproductive and individual status (i.e., dominance), security, and human disturbance (Schwartz et al. 2003). Average seasonal, annual, and life ranges for grizzly bears that have access to dependable, high-quality food resources are typically smaller than those in populations that do not have access to reliable concentrated food sources (Schwartz et al. 2003). Differences in annual-range size among study areas have been attributed to differences in habitat quality (McCloughlin and Ferguson 2000; McLoughlin et al. 2003). By season, spring and early summer ranges of females with cubs are often the smallest, attributed to lack of mobility of young cubs and/or security requirements (Aune and Kasworm 1989; Blanchard and Knight 1991; Dahle and Swenson 2003a,b). Late-summer and fall ranges are typically more variable. I posed the following questions:

1) are home range sizes related to movement rates of wolves and grizzly bears?;

2) how are home ranges of wolves and grizzly bears related to habitat productivity?;

3) how might pack size and pup rearing influence movement rates and home ranges of wolves?; and

4) how do movement rates and home ranges of grizzly bears vary with family status?

Objective 2. To document the dynamics of habitat selection by predators in the Besa-Prophet study area in relation to habitat type, habitat quality/productivity, and measures of habitat quality for prey species.

Resource selection functions (RSFs) (Boyce and McDonald 1999) use logistic regression to integrate knowledge and available data on animal locations (based on radiotelemetry and GPS technology), environmental variables (measured and remotely sensed), and human-related factors. Broad-scale information describing wildlife-habitat associations informs researchers about patterns of wildlife distribution across the landscape, but how an animal uses the landscape at finer grains, such as local movement patterns and habitat use within a home range, can provide potential indications of the underlying dynamics that structure communities. RSFs, in combination with GIS, remote-sensing imagery, and GPS technology, can be useful tools to address these questions. Habitat use can be analyzed at many different levels, where use and availability are estimated on different spatial scales (Johnson 1980). Although wolves occupy a wide variety of habitats (Mech 1995; Mladenoff et al. 1995, 1999), they may nevertheless show habitat affinity at fine scales such that habitat value could be expected to change within the broadly defined ecoregions of a regional landscape (Ciucci et al. 2003). Similarly, grizzly bears select fine-scale attributes from within broad-scale ranges such as elevational movements, and seasonal shifts in habitat use and selection related to plant phenology (Servheen 1983; Waller and Mace 1997) or the availability of specific plant resources (e.g., seeds of whitebark pine,

Pinus albicaulis) (Blanchard and Knight 1991; Felicetti et al. 2003a). My research addressed the following questions:

1) as a recognized habitat generalist, can patterns of habitat use and selection that are driven by specific habitat types be identified for wolves?;

2) in the absence of information on prey density, can patterns of habitat selection be identified to show that wolves use the landscape in response to vegetation productivity or quality that may influence prey distributions?;

3) is the analysis of 3rd-order habitat selection by wolves and grizzly bears useful to broad-scale management objectives?; and can empirical models developed at this scale improve upon or complement existing habitat suitability/capability models developed by the BC provincial government?;

4) is habitat selection by grizzly bears driven by specific habitat types, or more broadly by overall vegetation productivity or quality?;

5) are grizzly bears responding to relative habitat quality for available ungulate prey?; and

6) how is habitat selection by grizzly bears influenced by breeding status?

Objective 3. To determine the relative prey concentrations in the diets of wolves and grizzly bears in the Besa-Prophet study area.

Diets of wolves in a majority of studies have been determined by scat analysis (Spaulding et al. 2000). More recently, stable-isotope analysis has been increasingly used to quantify the relative contributions of prey items in carnivore (Ben-David et al. 1997; Roth 2002) and bear diets (Hildebrand et al. 1996). Scat analysis can identify specific prey items in the diet, but this technique is biased by differential digestibility of prey items (Roth and Hobson 2000). Stable-isotope analyses can provide better estimates of the dietary contribution of different prey species to predator dynamics, and contribute to a better understanding of the structure and dynamics of ecological communities (Kelly 2000; Post 2002; McCutchan et al. 2003). Stable-isotope techniques have the potential to provide a

more accurate measure of trophic position and to capture complex interactions such as omnivory, because they can track and integrate the assimilation of energy or mass flow through trophic pathways and ecological communities (Post 2002). Therefore, a combination of scat and stable isotope analyses probably provides the best resolution regarding predator diets (Hildebrand et al. 1996). I posed three general sets of questions regarding food habits of predators in the Besa-Prophet:

> 1) what are the primary components in the diets of wolves and grizzly bears, and how does prey composition vary seasonally and annually?; and when are prey species important to grizzly bears in this mountain system?;
>
> 2) what are the limitations of stable isotope analyses in diet reconstruction, and how might these weaknesses be addressed to better understand the autecology of predators?; and
>
> 3) how might stable isotope analysis and resource selection studies complement one another in defining interactions across a landscape in a manner suitable for making management decisions?; and can the techniques be combined to better identify mechanisms of niche differentiation of sympatric predators, either spatially and/or temporally?

Organization of Thesis

I arranged this thesis in four independent chapters prepared as submissions for peer-reviewed publication. These are preceded by the introduction and followed by a chapter on considerations for the conservation of top predators. Although I have written this thesis in the first person, the work was supported by the help of many people. It reports on the predator component of a group effort to understand the predator-prey dynamics of the Besa-Prophet area, and it has incorporated the contributions of many. Published versions of Chapters 2 through 5 will acknowledge major contributions with co-authorships. The first thesis objective on variations in home ranges and movement rates of wolves and grizzly bears is incorporated in Chapter 2 (*Variation in Annual and Seasonal Home Ranges of*

Grizzly Bears and Wolves in Relation to Movement, Habitat Productivity, and Breeding Status). The second objective describing habitat use and selection by wolves and grizzly bears is addressed in Chapter 3 (*Habitat Selection by Wolves (Canis lupus) in a Multi-Prey Ecosystem in the Northern Rocky Mountains of British Columbia*) and Chapter 4 (*Spatial and Temporal Variation in Habitat Selection by Grizzly Bears in Northern British Columbia*). The third objective characterizing prey selection and diet composition of wolves and grizzly bears is detailed in Chapter 5 (*The Use of Stable Isotopes of Carbon and Nitrogen to Infer Large-Mammal Predator-Prey Relationships*), which also challenges some of the assumptions inherent in the use of stable isotope models to reconstruct diets. The final chapter synthesizes the findings of this empirical approach, and presents these findings in the context of current habitat suitability models developed by the province of BC.

Chapter 2: Variation in Annual and Seasonal Home Range Sizes of Grizzly Bears and Wolves in Relation to Movement, Habitat Productivity, and Breeding Status

Introduction

The home-range is the normal area that an animal uses over a specified period of time to carry out the activities of securing food, mating, and caring for young (Burt 1943). Home ranges, and the movements within them, reflect the ecological requirements of animals because they include all of the resources that are used by a resident (Seaman and Powell 1990). Therefore, a home range describes the relationship between an individual's spatial movements and time (McLoughlin and Ferguson 2000). Defining what determines home-range size is complicated because of the immensely integrative nature of the home range (McLoughlin et al. 2003). It was first suggested that home range may be partially related to an animal's metabolic rate (McNab 1963). Subsequent studies have shown that other factors can influence the size of the area, such as social organization (Damuth 1981), population density (Wolff 1985; Desy et al. 1990; Wolff 1993; Wolff and Schauber 1996; Adler et al. 1997; Dahle and Swenson 2003b), risk of predation (Desy et al. 1990; Tufto et al. 1996), body mass (Harestad and Bunnell 1979), age (Cederlund and Sand 1994; Dahle et al. 2006), and reproductive status (Dahle and Swenson 2003a,b). Habitat quality, which includes abundance and predictability of food in time and space, is also an important factor influencing home range size because survival and reproduction are often food-limited (McLoughlin and Ferguson 2000; McLoughlin et al. 2003).

Home-range size of grizzly bears (*Ursus arctos*) is a function of habitat quality and population density (Nagy and Haroldson 1990). Sizes of ranges vary among regions in North America (Pearson 1975; Craighead 1976; Reynolds 1976; Nagy and Russell 1978; Russell et al. 1979; Reynolds and Hechtel 1980; Nagy et al. 1983a,b; Nagy et al. 1988),

among sex, age, and reproductive classes within regions (Pearson 1975; Nagy et al. 1983a,b; Dahle and Swenson 2003a,b; Dahle et al. 2006), and among classes of bears when changes occur in habitat quality (Pearson 1977; Reynolds and Hechtel 1980; Knight et al. 1984; McLoughlin et al. 1999; McLoughlin and Ferguson 2000), topographic structure (Pearson 1977; Hamer and Herrero 1983), and density associated with population growth or exploitation (Young and Ruff 1982).

Territoriality is defined as the active defense (e.g., fighting, song, or scent) of a home range or portion of a home range to the exclusion of conspecifics (Begon et al. 1990). The degree of territoriality exerted by individuals (or social groups) may be measured as the degree to which home ranges overlap (McLoughlin et al. 2000). Average sizes of home ranges and the extent to which they overlap can be highly variable among populations within a species (McLoughlin et al. 2000). Home-range size of wolves (*Canis lupus*) can vary 14-fold among areas (Fuller et al. 2003). Average territory size and the area available per wolf vary most directly with food resources or prey abundance, as well as with prey type and the mean annual rate of population change (Fuller et al. 2003). In general, the higher the prey density, the smaller the territory.

I report seasonal variation in movement rates and home-range sizes of adult female grizzly bears and wolves in the Besa-Prophet region of the northern Rocky Mountains, British Columbia (BC). I report basic range sizes and movement rates for comparative purposes to other studies. I also examine possible explanations for variation in seasonal and annual home-range sizes. I used global positioning systems (GPS) and geographic information systems (GIS) to examine spatial patterns in relation to habitat class and productivity and family status of grizzly bears, and in relation to habitat class and

productivity, and pack sizes of wolves. I predicted that whether a female grizzly bear was solitary or accompanied by cubs and the ages of those cubs would influence movement rates and the areas used. For wolves, seasonal ranges and movement rates were expected to vary closely with the breeding cycle. Wolves breed during winter when snow depths are also at their maximum, and as a result, wolves should use movements that minimize energy expenditures. During spring and summer months, prey availabilities should dictate movement patterns and areas used during a time when pup mobility is restricted to den and rendezvous sites. Movements of a wolf pack should be the least restricted during the fall months when pups are nearly fully grown and traveling with the pack. In addition to addressing ecological questions associated with changes in range sizes, this chapter sets the framework for subsequent analyses on resource use (Chapters 3 and 4) and defines the amount of space used by each grizzly bear and wolf pack, which subsequently should influence decisions of resource selection.

Study Area

The Muskwa-Kechika Management Area in northern BC covers approximately 6.4 million ha. My research occurred in the Besa-Prophet study area (BP), which includes the 204,245-ha Besa-Prophet pre-tenure planning area (a zone managed for oil and gas exploration and development), the 80,771-ha Redfern-Keily Provincial Park adjacent to and southwest of the Besa-Prophet pre-tenure planning area, and portions of surrounding areas. Three biogeoclimatic zones are found within the region (Meidinger and Pojar 1991): the boreal white and black spruce (BWBS) zone characterized by white and black spruce (*Picea glauca* and *P. mariana*) at low elevations, the spruce-willow-birch (SWB) zone of sub-alpine spruce, willow (*Salix sp.*), and birch (*Betula glandulosa*), and alpine tundra (AT)

generally at elevations >1600 m. The BWBS zone only accounts for approximately 3% of the BP. The SWB zone is the most northerly sub-alpine zone in BC and occupies the middle elevations of the northern Rocky Mountains, ranging between 900 m and up to the AT zone. Lower elevations of the SWB are generally forested, mainly by white spruce. Typically in many valleys in the SWB zone, there is intermittent to closed forest cover of white spruce and variable amounts of lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) in the valley bottoms and on lower slopes. The SWB zone covers ~81% of the land area in the BP. The remaining 16% of the BP is in the AT zone. The alpine zone is treeless, unless trees are in stunted or krummholz form. Alpine vegetation is dominated by a dwarf scrub of prostrate woody plants and some herbs, bryophytes, and lichens, but much of the alpine landscape consists of rock, ice, and snow. In the BP, *Dryas* spp. and *Cassiope* spp. are the dominant dwarf scrub vegetation in this zone.

The topography in the BP is an interlaced network of north-south ridges and east-west valleys with a prominence of south-facing slopes. This area supports one of the most diverse large-mammal predator-prey ecosystems in North America. Ungulates include moose (*Alces alces*), elk (*Cervus elaphus*), caribou (*Rangifer tarandus caribou*), Stone's sheep (*Ovis dalli stonei*), and mountain goats (*Oreamnos americanus*). Predators capable of preying on these ungulates include wolves, grizzly bears, black bears (*Ursus americanus*), cougars (*Felis concolor*), coyotes (*Canis latrans*), and wolverines (*Gulo gulo*), although it is believed that only wolves and grizzly bears are of sufficient numbers to be capable of limiting or regulating ungulate communities (Bergerud and Elliott 1998).

Methods

Captures and Locational Data

Twenty-seven grizzly bears were captured and fitted with GPS collars (Simplex, Televilt, Sweden) between May and June 2001-2003. Male bears shed their collars and, therefore, the few data from males were not suitable for analysis. Twenty-six wolves from 5 packs (Pocketknife, Lower Besa, Nevis, Dopp, Richards) were captured and fitted with similar collars during December 2001, March and April 2002, and March 2003. Both the Dopp and Richards packs shifted their territories and pack membership in 2003 and were renamed the Keily and Prophet packs respectively. At least 2 and up to 4 collars were deployed in a pack at any given time to account for the possibility of collar failure and dispersal. I programmed all GPS collars to acquire locations every 6 hr for 2-3 years on bears and 2 years on wolves. I secured GPS data via remote download or collar retrieval. I present data acquired from 13 female grizzly bears for which complete years (1-4 years) of GPS locations were available. For wolf packs, I randomly selected only one of a set of duplicate locations (i.e., same date and time) for analysis to avoid issues of dependence and biases associated with inflated sample sizes.

Home Ranges and Movement Rates

In my analyses, I identified 3 seasons for bears based on plant phenology: spring (den emergence to 15 June), summer (16 June - 15 August), and fall (16 August to denning). I identified 5 seasons for wolves based on biological criteria: winter (1 January - 28 February, breeding and peak snow depth), late winter (1 March - 31 April, pre-denning activities), denning (1 May - 31 July, pup-rearing and ungulate calving), late summer (1

August - 31 September, nursery stage when pups are physically immature and nurse at rendezvous sites), Fall (1 October - 31 December, when pups are almost fully grown and traveling with the pack).

From GPS locations of grizzly bears and wolves, I estimated sizes of annual home ranges using the 95% annual minimum convex polygon (MCP) method (Mohr 1947) (animal movement extension in ArcView version 3, Environmental Systems Research Institute, Redlands, California, USA) given that 5% of locations at the periphery of a home range related to extra-territorial movements may arbitrarily increase home ranges by 30 to 100% (Milakovic and Parker, unpub. data; Kernohan et al. 2001). To facilitate comparisons among populations in other regions, I also report home-range estimates using the 95% and 100% fixed kernel (The Home Ranger v. 1.5, F.W. Hovey, Ursus Software, Revelstoke, BC, Canada) technique with least squares cross-validation (LSCV) to determine bandwidths (Worton 1995; Seaman et al. 1998, 1999; Powell 2000; Belant and Follman 2002). Seasonal home ranges of grizzly bears and wolves were defined by the 100% MCP.

Only consecutive 6-hr fixes were used to estimate the seasonal movement rates of grizzly bears and wolves. Distances between consecutive GPS fixes were converted to distances in meters moved per 6 hours (m/6hr). For wolves, I used one-way ANOVA (Stata 9.2, StatCorp, Texas, USA) to separately examine movement rates and home ranges of wolves with season (5 seasons) used as the fixed effect. For grizzly bears, I used one-way ANOVA to separately examine movement rates and home ranges with season (3 seasons) and reproductive status (4 possible family groups: lone females, females with cubs-of-the-year, females with yearlings, females with 2-year olds) entered as fixed effects. Following a significant ANOVA result, I used Tukey's HSD test to identify individual pairwise

differences. I used linear regression to examine the relationship between seasonal home ranges and seasonal movement rates.

Habitat Assessment

Vegetation classes in the BP were identified using an August 2001 Landsat Enhanced Thematic Mapper 7 image and classified based on 227 field training sites (Lay 2005). The initial 15 vegetation classes (overall classification accuracy of 77%) were combined into 10 major habitat classes (Table 2.1). Classes were lumped according to similarity of vegetation and elevation, and possible prey associations (e.g., moose and riparian spruce; elk and deciduous burns; caribou and open alpine; sheep and *Elymus* burns). I then calculated the area of each habitat class that was available within the annual home ranges of grizzly bears and wolves using remote-sensing software (Geomatica 9.0, PCI Geomatics, Richmond Hill, Ontario). Annual and seasonal ranges were subsequently related to relative habitat proportions, and additionally to pack size of wolves.

Numerous studies have found that seasonal differences in multi-temporal Normalized Difference Vegetation Index (NDVI) values can be important in explaining movements of wildlife species (e.g., Lay 2005). The Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) onboard the Landsat satellites capture multi-spectral data at 30-m resolution. Lay (2005) used 14 TM and ETM+ images to generate NDVI images during the growing season for 3 years (2001-2003) in the BP. NDVI is correlated with plant biomass (Tucker and Sellers 1986, Ruimy et al. 1994). The spectral signatures of NDVI comprise a major contribution from understory vegetation and not just the overstory component of treed species (Lay 2005). To explore the relationship between habitat productivity (as compared to habitat proportions alone) and sizes of annual home ranges of

Table 2.1. Habitat classes used in analyzing home-range associations of grizzly bears and wolves in the Besa-Prophet study area of northern British Columbia.

Habitat Class	Description
Conifer	Dense mid-elevation pine (*Pinus contorta*) and spruce (*Picea glauca*) stands.
Stunted Spruce	Open spruce areas typical of northerly slopes.
Shrub	Willow (*Salix* spp.) and birch (*Betula glandulosa*) shrub communities ≤1600 m.
Alpine Shrub	Willow and birch shrub communities above 1600 m.
Non-Vegetated	Rock (boulder, talus), rock-lichen associations, water, snow.
Riparian Spruce	Low elevation (<1600 m) wetland spruce (*P. glauca* or *P. mariana* in poorly drained sites) along streams; includes gravel bars and sedge (*Carex* spp.) meadows.
Open Alpine	Dry alpine tundra habitat >1600 m characterized by *Dryas* spp.; wet alpine tundra habitat > 1600 m dominated by *Cassiope* spp. and sedge (*Carex* spp.) meadows.
Deciduous Burns	Older burns; characterized by deciduous shrubs and regenerating young aspen/poplar (*Populus tremuloides* and *P. balsamifera*) stands.
Elymus Burns	Younger burns; meadows dominated by *Elymus innovatus*.
Sub-alpine Spruce	Open spruce; transition zone between dense mid-elevation spruce stands and open alpine areas.

grizzly bears and wolves, I multiplied the area of each habitat class by the respective mean NDVI values for a particular season to obtain a standardized index of relative habitat biomass or productivity. For grizzly bears, I used peak NDVI values during June to represent spring plant biomass, peak NDVI values during July to represent summer plant biomass, and peak NDVI values during September to represent fall plant biomass. For wolves, adequate NDVI data were available only for the denning and late summer seasons. Additionally, I divided the product of habitat area and NDVI by pack size to represent an index of habitat productivity per wolf.

I used multiple forward-stepwise regression to explore the relationship between sizes of annual and seasonal home ranges of grizzly bears and wolves and the proportion of habitat classes and habitat productivity within those ranges. The entry probability in my study differs from the general advice of Hosmer and Lemeshow (2000) of including covariates at a probability of 0.20 because I wanted to avoid over-fitting, and to restrict the analysis to exploring independent variables that contributed most significantly to variation in the dependent variable (i.e., home-ranges, Oakleaf et al. 2003; Trapp 2004; Rauset 2006). I began with a level of entry set at $P < 0.05$ to identify significant variables. In cases where no variables were entered into the model, I relaxed the entry criteria down to $P < 0.10$ or < 0.15 to identify variables that *may* be important to explaining variation in home range size. The intent here was to explore the relative contribution of a few potentially important habitat classes to home-range size, not to generate a predictive model. Candidate variables were assessed for multi-collinearity at a tolerance level of 0.30 (Hosmer and Lemeshow 2000) prior to incorporation in the regression analyses.

Results

Grizzly Bears

Annual

I retrieved 13,570 GPS locations from 13 female grizzly bears between June 2001 and October 2004. I observed a 67% ± 12% fix rate ($\overline{X}$ ± SE; range = 26 - 87% across individuals) across seasons and years. There was no correlation between sample size and sizes of annual MCP ranges ($r = 0.35$, $P = 0.53$) or seasonal MCP ranges ($r = 0.14$, $P = 0.21$). Annual 95% MCP range ($\overline{X}$ ± SE; 334 ± 33 km^2, range: 82 - 662 km^2) and 100% fixed kernel home range (306 ± 31 km^2, range: 79 - 606 km^2) estimates were similar (Table 2.2). By family group, annual MCP home ranges averaged 280 km^2 for females with cubs of the year (82 - 529 km^2, N = 9), 374 km^2 for females with yearling cubs (188 - 662 km^2, N = 9), 292 km^2 for females with 2-year old cubs (236 - 360 km^2, N = 3), 275 km^2 for sub-adult bears (191 - 370 km^2, N = 3), and 375 km^2 for lone adults (267 - 511 km^2, N = 7). Annual means were not a function of family status ($F_{3, 27} = 0.92$, $P = 0.44$). Female grizzly bears in the BP showed high fidelity to annual ranges and shared their ranges with as many as 4 other collared female bears, with the extent of overlap varying from a portion at the edge of a range to complete co-occurrence (Figures 2.1 and 2.2). Incorporating NDVI as an index of habitat productivity explained a higher degree of variation in mean annual home range sizes of grizzly bears than habitat proportions alone (Table 2.3). Overall, the signs of the coefficients suggest that the average sizes of individual annual home ranges are inversely related to the extent of *Elymus* burns, and proportional to the extent of open alpine, non-vegetated, and conifer habitats.

Table 2.2. Annual minimum convex polygon (MCP) and fixed kernel home ranges of individual grizzly bears in the Besa-Prophet study area of northern British Columbia, presented with family status by year. COY = cubs of the year, juveniles = 2-year olds.

Bear	Year	Family Status	Annual Home Range (km^2)			*N*
			95% MCP	95% Fixed Kernel	100% Fixed Kernel	
G01	2001	2 Yearlings	188	122	210	389
	2002	2 Juveniles	279	153	268	418
	2003	With Male	511	238	409	465
	2004	2 COY	82	45	79	443
G05	2001	2 COY	126	59	105	602
	2002	2 Yearlings	194	86	162	493
	2003	2 Juveniles	236	89	167	272
	2004	2 COY	no data			
G08	2001	With Male	492	285	508	338
	2002	With Male	454	184	381	364
	2003	3 COY	529	250	495	508
	2004	3 Yearlings	662	326	610	330
G15	2001	Alone	no data			
	2002	With Male	no data			
	2003	2 COY	130	76	120	371
	2004	2 Yearlings	289	166	280	288
G18	2001	1 Yearling	478	287	454	496
	2002	With Male	no data			
	2003	2 COY	493	230	378	489
	2004	2 Yearlings	474	242	415	378
G20	2002	Sub-Adult	370	206	333	422
	2003	With Male	267	181	278	371
	2004	1 COY	no data			
G21	2002	2 COY	423	160	306	375
	2003	2 Yearlings	582	350	606	378
G22	2002	3 Juveniles	360	246	398	438
	2003	2 COY	285	203	344	398
G23	2002	Sub-Adult	191	81	141	230
	2003	With Male	378	140	254	125
	2004	Alone	no data			
G24	2002	Sub-Adult	264	142	258	394
	2003	Alone	394	212	373	303
G25	2002	2 COY	119	66	113	458
	2003	2 Yearlings	219	124	212	537
G26	2003	3 COY	336	196	338	461
	2004	3 Yearlings	284	178	305	388
G27	2003	With Male	429	196	346	359

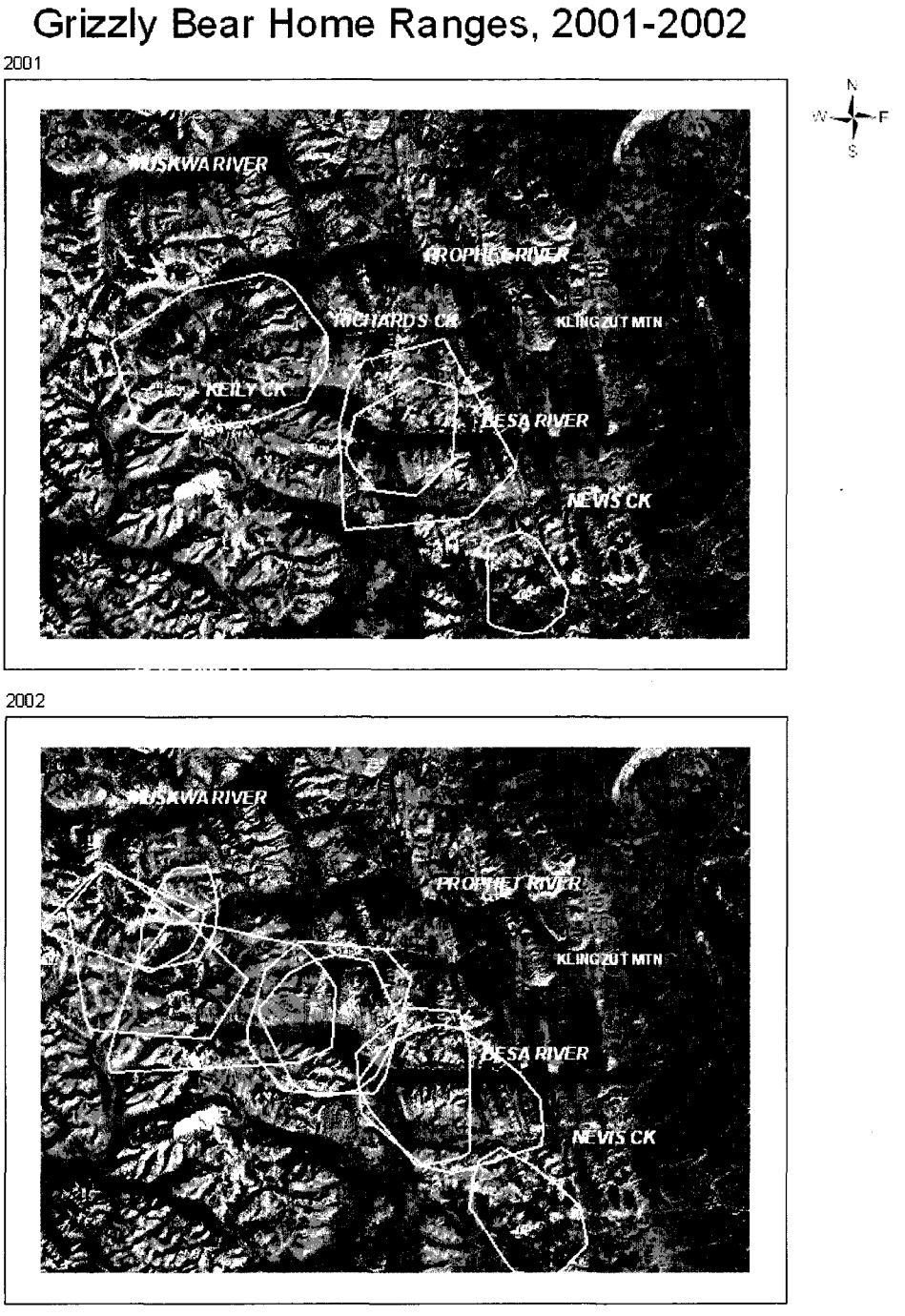

Figure 2.1. Annual home ranges, as defined by 95% minimum convex polygon (MCP), of female grizzly bears in the Besa-Prophet study area of northeastern British Columbia, 2001-2002. Area shown covers approximately 75 x 100 km.

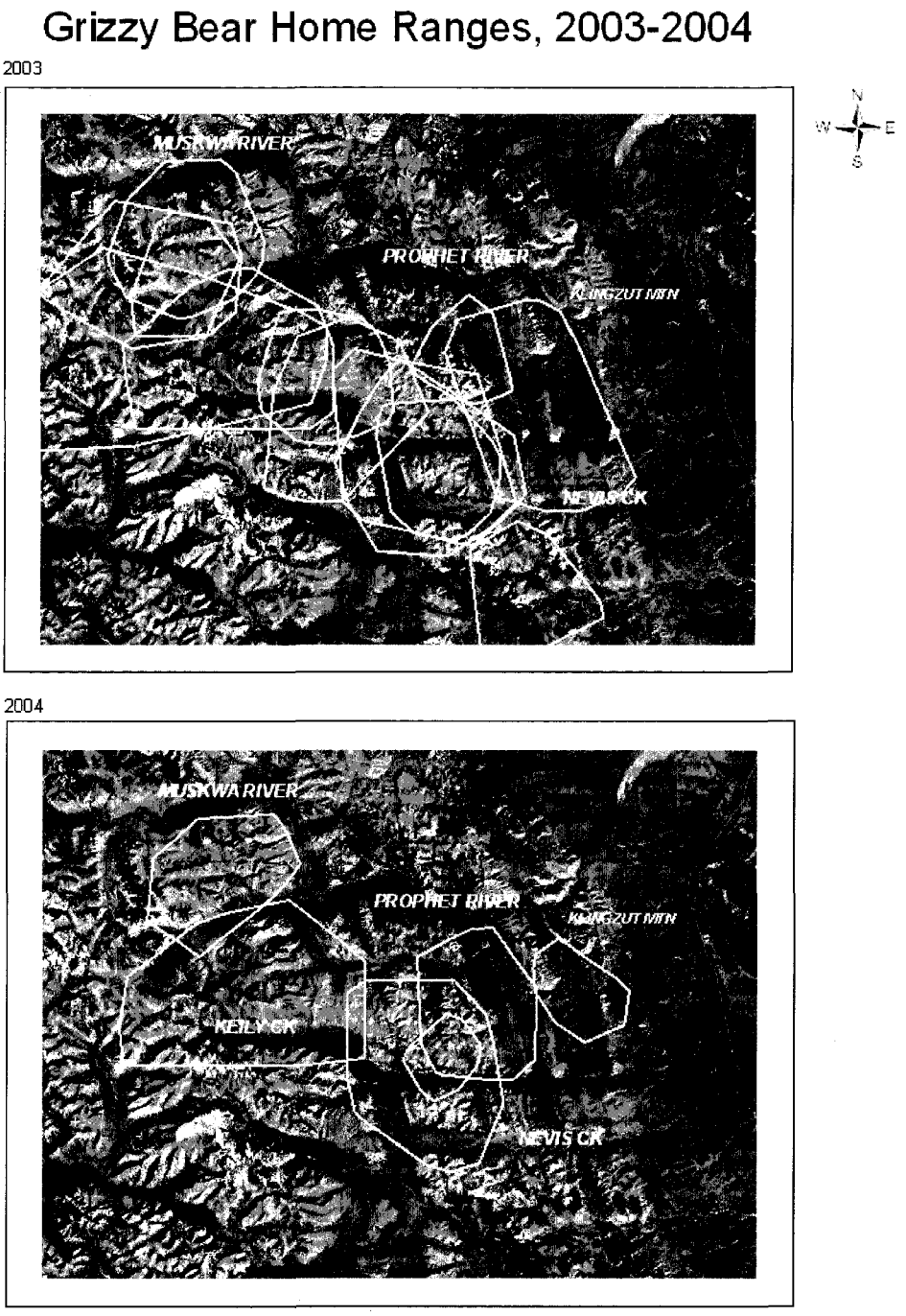

Figure 2.2. Annual home ranges, as defined by 95% minimum convex polygon (MCP), of female grizzly bears in the Besa-Prophet study area of northeastern British Columbia, 2003-2004. Area shown covers approximately 75 x 100 km.

Table 2.3. Results of stepwise regression relating mean annual and seasonal home ranges of female grizzly bears in the Besa-Prophet study area of northeastern British Columbia to the proportional habitat extents within each range, unweighted (habitat proportion) and weighted (productivity) by the Normalized Difference Vegetation Index (NDVI). Level of entry of stepwise regressions is 0.05 unless otherwise stated. Coefficients represent the magnitude and direction of the relationship between habitat class and home range.

Range	Model	F	*P*	Adj R^2
ANNUAL:				
Habitat Proportion	(-101.43) *Elymus* Burns (-30.46) Alpine Shrub (+41.30) Open Alpine	$F_{(3,9)} = 11.38$	0.002	0.72
Productivity (Habitat Proportion x NDVI)	(-190.96) *Elymus* Burns (+67.58) Open Alpine (+12.32) Non-Vegetated (+11.88) Conifer	$F_{(4,8)} = 78.69$	<0.001	0.81
SEASONAL:				
Habitat Proportion				
Spring[a]	(-70.86) *Elymus* Burns (+36.96) Deciduous Burns	$F_{(2,9)} = 4.87$	0.037	0.41
Summer[a]	(-28.82) *Elymus* Burns (+5.02) Conifer	$F_{(2,10)} = 4.94$	0.032	0.40
Fall	(-34.19) *Elymus* Burns	$F_{(1,11)} = 7.51$	0.019	0.35
Productivity (Habitat proportion x NDVI)				
Spring[a]	(-39.95) *Elymus* Burns	$F_{(1,10)} = 4.49$	0.069	0.27
Summer[b]	(-35.63) *Elymus* Burns (+17.37) Stunted Spruce	$F_{(2,10)} = 4.60$	0.024	0.38
Fall	(-50.08) *Elymus* Burns	$F_{(1,11)} = 8.11$	0.016	0.36

[a] level of entry $P < 0.10$
[b] level of entry $P < 0.15$

Seasonal

Sizes of seasonal ranges of grizzly bears were partially a function of habitat class (Table 2.3). Plant biomass as indexed by NDVI did not appear to influence seasonal range sizes as the index did not explain a greater variation in seasonal range sizes. Across seasons, ranges were inversely related to the extent of *Elymus* burns. Additionally, spring ranges were larger when there was more deciduous burn habitat, and summer ranges were proportional to the extent of conifer habitat.

Seasonal home ranges and movement rates were highly variable among individual (Appendix A, Figure A1). During the spring, female grizzly bears used an average of 182 km^2 (range: 19 - 346 km^2) and moved an average of 1.1 km/6hr (range: 0.1 – 2.7 km/6hr). Summer occupancy by female grizzly bears averaged 223 km^2 (range: 72 - 413 km^2) while they moved an average of 1.3 km/6hr (range: 0.4 – 2.0 km/6hr). Female bears tended to roam most widely during the fall with average home ranges of 244 km^2 (range: 45 - 452 km^2) and average movement rates of 1.4 km/6hr (range: 0.4 - 2.5 km/6hr). Seasonal differences in home ranges ($F_{2, 82} = 1.64$, $P = 0.20$) and movement rates ($F_{2, 82} = 2.19$, $P = 0.12$), however, were not statistically significant.

Sizes of seasonal ranges ($F_{3, 81} = 3.92$, $P = 0.01$) and movement rates ($F_{3, 81} = 7.29$, $P < 0.001$) appeared to be a function of family status (Table 2.4; Appendix A, Figure A2). Females with cubs of the year used significantly less area ($\overline{X}$ = 101 km^2) than females with yearlings ($\overline{X}$ = 243 km^2, $P = 0.012$) and lone adults ($\overline{X}$ = 279 km^2, $P = 0.007$) during the spring. Females with cubs also moved significantly less during the spring ($\overline{X}$ = 0.6 km/6hr) than females with yearlings ($\overline{X}$ = 1.1 km/6hr, $P = 0.002$), females with 2-year olds ($\overline{X}$ = 0.9 km/6hr, $P = 0.001$), or lone adults ($\overline{X}$ = 1.6 km/6hr, $P < 0.0001$). This trend

Table 2.4. Sizes of seasonal home ranges and movement rates, with standard errors ($\bar{X}$ ± SE), of female grizzly bears in the Besa-Prophet study area of northeastern British Columbia. Seasonal ranges are 100% MCPs. Data are pooled by family status, across years and individuals. COY = cubs of the year. Juveniles = 2-year olds.

Family Status	Season	Movement Rate (km/6hr)		Home Range Size (km^2)		*N*
		$\bar{X}$ ± SE	Range	$\bar{X}$ ± SE	Range	
COY	Spring	0.63 ± 0.08	0.10 - 1.07	101 ± 38	19 - 327	9
	Summer	0.89 ± 0.07	0.43 - 1.23	171 ± 34	72 - 331	9
	Fall	1.29 ± 0.21	0.38 - 2.51	217 ± 50	45 - 412	9
Yearlings	Spring	1.15 ± 0.19	0.64 - 1.90	243 ± 42	74 - 436	8
	Summer	1.31 ± 0.11	0.76 - 1.66	253 ± 42	109 - 413	9
	Fall	1.54 ± 0.21	0.73 - 2.36	249 ± 50	86 - 436	8
Juveniles	Spring	0.85 ± 0.21	0.68 - 0.95	130 ± 46	108 - 150	3
	Summer	1.45 ± 0.11	1.21 - 1.83	233 ± 35	132 - 345	3
	Fall	1.25 ± 0.11	1.00 - 2.06	193 ± 24	141 - 276	3
Alone	Spring	1.62 ± 0.17	1.24 - 2.03	279 ± 35	125 - 346	5
	Summer	1.54 ± 0.11	1.06 - 1.90	252 ± 37	117 - 410	7
	Fall	1.37 ± 0.22	0.73 - 1.93	307 ± 40	191 - 452	6

continued through the summer when females with cubs moved, on average, 0.9 km/6hr, which was less than females with yearlings ($\overline{X}$ = 1.3 km/6hr, $P = 0.002$), females with 2-year olds ($\overline{X}$ = 1.4 km/6hr, $P = 0.001$), and lone adults ($\overline{X}$ = 1.5 km/6hr, $P < 0.0001$).

Seasonal range sizes of female grizzly bears were partially a function of respective movement rates of individuals by year and season ($r^2 = 0.33$), by individual and season ($r^2 = 0.33$), and only during the fall when pooled across seasons ($r^2 = 0.42$) (Table 2.5). When grouped by family status, a greater proportion of the variation in seasonal range sizes was explained by seasonal movement rates ($r^2 = 0.72$).

Wolves

Annual

I retrieved 7,447 GPS locations from 25 collared wolves in 5 packs between December 2001 and September 2004. I observed a 61% ± 3% fix rate ($\overline{X}$ ± SE; range = 52 - 70% for 7 packs) across seasons and years. There was no correlation between sample size and annual MCP home range ($r^2 = 0.02$, $P = 0.91$) or seasonal MCP ranges ($r^2 = 0.01$, $P = 0.62$). There was general agreement between annual 95% MCP ranges ($\overline{X}$ ± SE; 801 ± 118 km^2) and 100% fixed kernel home-range (778 ± 174 km^2) estimates (Table 2.6). Pack sizes varied between 2 and 17. Despite the limitations of MCP boundaries, overlap in annual territories was not extensive between packs (Figure 2.3). Annual home-range sizes were inversely related to the extent of alpine shrub habitat with and without the NDVI weighting. Given that both models explained a similar amount of variation in range sizes, the influence of the habitat productivity may be minimal (Table 2.7). Models that were adjusted for pack size explained more variation in the sizes of pack ranges. The best model corrected for pack

Table 2.5. Linear regressions predicting sizes of seasonal home ranges of female grizzly bears (km^2) in the Besa-Prophet study area in northeastern British Columbia from movement rates (km/6hr), with data grouped as indicated by Term.

Term	Slope	Constant	F	*P*	r^2
Individual : Year : Season	143.33	45.10	$F_{(1,81)} = 57.48$	**<0.001**	0.33
Individual : Season	736.67	1.26	$F_{(1,36)} = 19.57$	**<0.001**	0.33
Season					
Spring	60.00	59.89	$F_{(1,10)} = 3.26$	0.100	
Summer	66.67	93.71	$F_{(1,11)} = 2.36$	0.150	
Fall	46.67	58.71	$F_{(1,11)} = 11.70$	**0.010**	0.42
Family Status : Season	20.00	24.56	$F_{(1,12)} = 69.29$	**<0.001**	0.72

Table 2.6. Sizes of annual minimum convex polygon (MCP) and fixed kernel home ranges of wolves in the Besa-Prophet study area of northern British Columbia. Five packs were followed between 2002 and 2004. The Richards and Dopp packs shifted their territories in 2003 and were renamed the Prophet and Keily packs, respectively. Pack sizes were variable during the course of this study. Reported sizes are the maximum number of individuals observed.

Pack	Year	Pack Size	Annual Home Range (km^2)			*N*
			95% MCP	95% Fixed Kernel	100% Fixed Kernel	
Pocketknife	2002	16	755	504	809	855
	2003	14	1333	877	1386	389
Lower Besa	2002	12	1069	655	1066	700
	2003	15	1173	791	1268	499
Nevis	2002	12	549	359	593	653
	2003	12	920	629	967	855
	2004	17	879	483	845	423
Richards	2002	8	1224	665	1189	772
Prophet	2003	6	476	264	477	731
	2004	6	603	334	582	304
Dopp	2002	8	780	510	865	741
Keily	2003	5	375	167	281	525

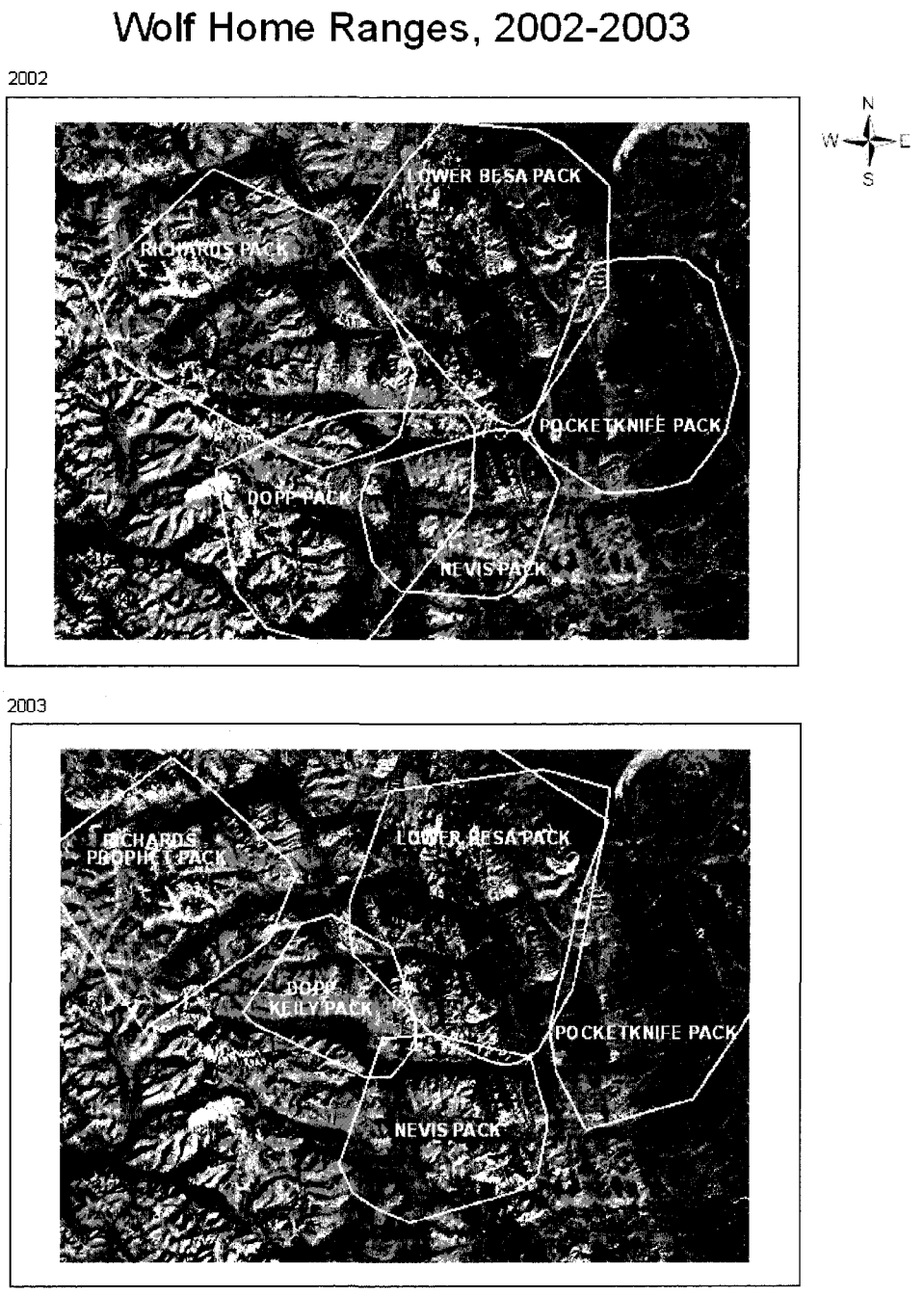

Figure 2.3. Annual home ranges, as defined by 95% minimum convex polygon (MCP), of wolves in the Besa-Prophet study area of northeastern British Columbia, 2002-2003. Area shown covers approximately 75 x 100 km.

Table 2.7. Results of stepwise regression relating sizes of annual and seasonal home ranges of wolves in the Besa-Prophet study area of northeastern British Columbia to the proportional habitat availabilities within each range, weighted by the Normalized Difference Vegetation Index (NDVI) as an index of habitat productivity, and corrected for pack size as an indicator of available habitat productivity per wolf. Pooled models are for the denning and late summer seasons. Level of entry $P < 0.05$.

Range	Term	Model	F	*P*	Adj R^2
ANNUAL	**Habitat proportion**	(-36.94) Alpine Shrub	$F_{(1,10)} = 7.84$	0.019	0.38
	Habitat proportion / pack size	(+50.97) Conifer	$F_{(1,10)} = 17.93$	0.002	0.58
	Productivity (relative habitat area x NDVI)	(-54.87) Alpine Shrub	$F_{(1,10)} = 7.95$	0.018	0.39
	Productivity / pack size	(+96.36) Conifer (+33.49) Riparian	$F_{(2,9)} = 12.72$	0.002	0.71
SEASONAL (all seasons)	**Habitat proportion**	(+8.71) Non-Vegetated (+41.72) Stunted Spruce (+39.65) Shrub	$F_{(3,28)} = 3.26$	0.036	0.18
	Habitat proportion / pack size	(+0.73) Non-Vegetated	$F_{(1,30)} = 12.99$	0.001	0.28
(denning, late summer)	**Habitat proportion**	(+30.76) Deciduous Burns	$F_{(1,10)} = 13.38$	0.004	0.53
	Habitat proportion / pack size	(-1.48) Riparian (-1.67) Alpine Shrub	$F_{(2,9)} = 5.23$	0.031	0.44
	Productivity (relative habitat area x NDVI)	(+36.41) Deciduous Burns	$F_{(1,10)} = 11.37$	0.007	0.49
	Productivity / pack size	(+70.81) Conifer	$F_{(1,10)} = 31.82$	<0.001	0.74

size indicated that annual ranges were proportional to the extents of both conifer and riparian habitats when NDVI was incorporated.

Seasonal

In contrast to the annual models, the combination of habitat proportion and pack size accounted for only 30% of the variation in seasonal ranges of wolves, and up to 54% of the variation in range sizes during the denning and summer seasons (Table 2.7). As a function of NDVI and pack size, wolf home ranges during the denning and late summer seasons were proportional to the extent of conifer habitat ($P < 0.001$, $R^2 = 0.74$). Within packs, differences in sizes of seasonal ranges varied from 39 to 1309 km^2.

Overall, movement rates ($F_{(4,27)} = 5.90$, $P = 0.002$) varied by season, but range sizes did not ($F_{(4,27)} = 0.81$, $P = 0.53$) (Table 2.8). Wolves ranged across 238 to 1205 km^2 during the winter and from 195 to 1388 km^2 during the late winter. At other times of the year, wolf packs ranged across 257 - 1132 km^2 during denning, 163 - 829 km^2 during late summer, and 310 - 837 km^2 during fall. Average movement rates by pack tended to peak during the denning period for all packs (Table 2.8; Appendix A, Figure A3), ranging from 2.9 to 8.7 km/6hr. The Pocketknife, Nevis, Richards/Prophet, and Dopp/Keily packs had the lowest movement rates during the winter or late winter seasons (1.9 to 2.6 km/6hr). The Lower Besa and Richards/Prophet (2002) packs had similar between-season movement rates (within 0.6 km/6hr), with the exception of the denning period. Considering all packs together, sizes of seasonal ranges were a significant function of movement rates during the winter, late winter, and denning periods (Table 2.9).

Table 2.8. Sizes of seasonal home ranges and movement rates of wolves in the Besa-Prophet study area of northeastern British Columbia. Data are presented by year. Seasonal ranges are 100% MCPs. Five packs were followed between 2002 and 2004. The Richards and Dopp packs shifted their territories in 2003 and were renamed the Prophet and Keily packs, respectively. Pack sizes are the maximum number of individuals observed. Range is km^2 and Rate is km/6hr.

Pack	Year	Pack Size	Winter		Late Winter		Denning		Late Summer		Fall	
			Range	Rate	Range	Rate	Range	Rate	Range	Rate	Range	Rate
Pocketknife	2002	16	657	2.4	400	1.9	399	4.0	411	3.5	706	3.4
	2003	14							309	15.3	406	4.2
Lower Besa	2002	12	596	3.6	730	2.5	734	4.6	829	10.1	310	2.9
	2003	15	289	2.4	685	3.6	458	4.5	564	3.0	837	3.4
Nevis	2002	12			355	1.8	315	3.2	272	2.7	410	2.9
	2003	12	417	2.0	595	2.1	548	4.4	596	2.6	758	2.6
	2004	17	584	1.9	597	2.7	598	4.3	559	3.6		
Richards	2002	8			527	3.3	1132	8.7	442	3.1	398	2.7
Prophet	2003	6	238	2.0	231	1.8	284	3.3	163	2.6	429	3.4
	2004	6	398	2.6	508	2.1	333	2.6				
Dopp	2002	8			289	1.9	449	4.5	425	3.5	559	3.7
Keily	2003	5	285	2.6	195	2.3	257	4.1	171	1.3		

Table 2.9. Linear regressions predicting seasonal home ranges (km^2) of wolves in the BP study area in northeastern British Columbia from movement rates (km/6hr), with data grouped as indicated by Factor.

Term	Slope	Constant	F	*P*	r^2
Pack : Year : Season	65.00	262.10	$F_{(1,45)} = 6.46$	**0.010**	0.10
Pack : Season	61.67	254.98	$F_{(1,29)} = 4.31$	**0.047**	0.12
Season					
Winter	55.00	299.26	$F_{(1,7)} = 148.44$	**<0.001**	0.76
Late Winter	91.67	246.15	$F_{(1,10)} = 225.21$	**<0.001**	0.78
Denning	33.33	340.73	$F_{(1,10)} = 9.67$	**0.010**	0.43
Late Summer	11.67	379.96	$F_{(1,9)} = 0.27$	0.610	
Fall	3.33	523.13	$F_{(1,7)} = 0.01$	0.980	

Discussion

My results support the hypotheses that family status of grizzly bears, and breeding status and pack size of wolves influence home-range sizes and movement rates. These factors appear to be operating at different scales, and should be considered more broadly in carnivore ecology studies. Annual home ranges of grizzly bears may be a function of habitat productivity, whereas the annual ranges of wolves appear to integrate both habitat productivity and pack size. Sizes of seasonal home ranges and movement rates, while marginally correlated with each other, varied with breeding status in both grizzly bears and wolves. These findings are consistent with observations from other studies that home range size is a highly integrative process whereby home range is influenced by numerous factors including food availability, patchiness in the environment, density, predation, and sex (McLoughlin and Ferguson 2000).

There has been some contention over which home-range estimates are most representative (sic. Collins et al. 2005), and I presented fixed kernel estimates for comparative purposes only. I based my analyses for both grizzly bears and wolves on MCP home ranges because they formed the basis of habitat selection studies (see Chapters 3 and 4). I used 95% MCP home-ranges because of sensitivity to outliers or extra-territorial movements (Kernohan et al. 2001). For the purpose of studying habitat selection, MCP boundaries may more appropriately reflect what is *available* to animals at the home range scale than kernel estimates. For both grizzly bears and wolves, there was no correlation between sample size and MCP estimates, and combined with the agreement with

100% fixed kernel estimates that integrate intensity of use, I believe that I have adequately captured the space used by individual grizzly bears and wolf packs in the BP.

Grizzly Bears

It is difficult to compare estimates of home-range size of grizzly bears among studies because of different methods used to collect data and calculate areas (Collins et al. 2005). Irrespective of the techniques used, however, mean annual home ranges of female grizzly bears in the BP, as measured by either the 95% MCP (334 km^2), 95% fixed kernel (176 km^2), or the 100% fixed kernel (306 km^2) were comparable to those reported for females (73 - 476 km^2) in other interior grizzly bear populations of Alaska (Ballard et al. 1982; Reynolds 1993), Yukon (LeFranc et al. 1987), Northwest Territories (Miller et al. 1982; McLoughlin et al. 1999), British Columbia (McLellan 1984; Woods et al. 1997; Ciarniello 2006), Alberta (Nagy et al. 1988; Carr 1989), Yellowstone National Park (Blanchard and Knight 1980; Knight et al. 1986), and Montana (Aune and Kasworm 1989; Mace and Waller 1998).

The spatial organization of grizzly bears in the BP, with the high degree of overlap in annual home ranges, is in general agreement with the space-use model for grizzly bears presented by McLoughlin et al. (2000). The model applies to food-maximizing, solitary-living animals, and predicts high home-range overlap in areas of high habitat quality as defined by the abundance and predictability of food resources. Sizes of annual home ranges of grizzly bears in the BP appear to be inversely related to the relative productivity (as measured by the product of available habitat and its NDVI value) of *Elymus*-dominated burns, which is a high-quality habitat favored by grizzly bears in the BP for its vegetative productivity and potential to encounter ungulate prey (see Chapter 4). Both the *Elymus*-(younger disturbance) and deciduous-dominated (older disturbance) burn categories include prescribed and natural fires, and other disturbed areas such as avalanche chutes that are

similarly characterized by high productivity and low-stature vegetation that is distinct in composition from wet and dry alpine areas, transition areas, and the shrub habitat classes. Avalanche chutes could not be differentiated spectrally from the burn classes (Lay 2005), but the number of avalanche chutes in the BP appears limited. Avalanche chutes have long been recognized as being important to grizzly bear populations (Ramcharin 2000). In general, sizes of annual home ranges for grizzly bears across North America are inversely related to annual primary productivity (McLoughlin et al. 1999). Increases in food availability allow organisms to obtain sufficient energy to meet life requisites within smaller home ranges (McLoughlin and Ferguson 2000). Smaller ranges may also be a product of increases in population densities that are associated with high habitat quality (McLoughlin and Ferguson 2000). Among barren-ground grizzly bears, spatial differences in habitat influenced home ranges (McLoughlin et al. 2003). Sizes of home ranges in these populations increased with increasing proportions of habitat not highly valued by grizzly bears, such as bedrock, wetland, and heath-boulder habitats. Conversely, sizes of home ranges decreased amongst bears that had access to higher value habitats near treeline. In the BP, annual home ranges appear to increase with higher proportions of relatively unproductive open alpine, non-vegetated, and conifer habitats.

Seasonal variation in space use and movement rates was a function of family status of grizzly bears in the BP as spring home ranges were smaller and spring and summer movements were significantly lower for sows with cubs than those in other family groups. Few studies have compared home ranges or movement rates among female grizzly bears of differing family status, and results to date have been inconclusive and focused on annual ranges. There were no differences in range size between grizzly bears with cubs of the year and older family groups in southcentral Alaska (Ballard et al. 1982), the Khutzeymateen

valley in British Columbia (MacHutchon et al. 1993), or the Northwest Territories (McLoughlin et al. 2003). McLoughlin et al. (2003) concluded that biologically significant differences among ranges of female grizzly bears of differing family status likely do exist, but differences may be only of short duration and hence difficult to test. In southern Yukon (Pearson 1975), northern Yukon (MacHutchon 1996), Yellowstone (Blanchard and Knight 1991), Northwest Territories (Nagy et al. 1983a), and my study, however, sizes of home ranges increased as cubs aged and after cubs dispersed.

Biological mechanisms underlying seasonal differences in home ranges and movements by female grizzly bears in relation to family status appear to be influenced by mortality risk to cubs, as opposed to mobility or forage quality. In Scandinavia, females with cubs restricted their range size during the mating season (May to early July) and increased their ranges during the post-mating season, and ranges of females with cubs were smaller than those of lone females and older family groups during the mating season (Dahle and Swenson 2003a). This latter study concluded that ranges and movements of female grizzly bears with cubs were driven by infanticide avoidance. The relative immobility of cubs could not explain size-restricted ranges because cubs are highly active shortly after den emergence, and movements were found to be density-dependent. In Alaska, females with cubs avoided concentrations of other bears, utilizing lower quality habitats (Suring et al. 2006), and could be found at higher elevations during the non-denning period (Collins et al. 2005). Although sexually selected infanticide may be operating in some North American grizzly bear populations (see McLellan 2005), it was not observed in the BP. During the course of this study, I documented only 1 case of a female grizzly being killed by another bear. Other bear mortalities were human-caused, and aside from these cases, cub survival was 100%. Habitat selection by female grizzly bears with cubs during the spring in the BP was driven by

elevation and slope as opposed to habitat class per se (Appendix D, Table D1), which may be linked to the avoidance of males or possibly wolves that utilize mid-elevation slopes (see Chapter 3). In habitats that are of higher overall quality, restricting movements and space use to minimize risks to cubs may not pose a significant tradeoff to replenishing or maintaining body condition.

Wolves

Mean annual home ranges of wolves in the BP, as measured by either the 95% MCP (801 km^2), 95% fixed kernel (447 km^2), or 100% fixed kernel (778 km^2) were comparable to those of other western North American populations that identified moose as the primary prey (424 - 1,645 km^2, Peterson et al. 1984; Ballard et al. 1987; Bjorge and Gunson 1989; Hayes et al. 1991; Gasaway et al. 1992; Ballard et al. 1997; Mech et al. 1998; Hayes and Harestad 2001a,b). When habitat productivity and pack size (or more accurately, the amount of space available per wolf) were taken into account, 74% of the variation in sizes of annual home ranges of wolves in the BP was explained by the proportional extent of conifer stands and riparian habitats, and 76% of the variation in seasonal range sizes during denning and late summer was explained by the proportional extent of conifer habitats alone.

In general, it has been found that average territory size varies with prey abundance, prey type, and mean annual rate of population change (Fuller et al. 2003). On average across North America, 33% of the variation in territory size and 35% of the variation in mean area per wolf can be attributed to variation in prey density (Fuller et al. 2003). In Wisconsin, as much as 59% of the variation in territory size was explained by prey density (Wydeven et al. 1995). Because sample sizes were small in my study, incorporating proportional habitat availabilities and pack size merits further investigation across studies, particularly in regions where multiple large ungulate prey species are available and used, as in the BP. In the

absence of density estimates of prey species, NDVI may serve as a surrogate for overall prey availability. NDVI is highly correlated with greenness (Tucker and Sellers 1986; Ruimy et al. 1994; Oindo 2002), and greenness has been shown to be correlated with ungulate density (Carroll et al. 2001b). This is consistent with the suggestion that NDVI may be used more appropriately at coarser grains of analyses that relate ungulate density to habitat *occupancy* by wolves (across annual and seasonal ranges), rather than for use and selection at smaller spatial scales (patch size) (see Chapter 3). Messier (1985) concluded that territory size was governed by a combination of pack size and prey density, and that modelling wolf territory on the basis of prey density without considering the concurrent influence of pack size should not be expected to reflect reality. Territory size is further constrained by wolf density and a pack's ability to defend its boundary.

Discounting the effects of extra-territorial movements (by using 95% MCP), there was little overlap in wolf annual ranges in the BP. Between 2002 and 2003, the Dopp and Richards packs shifted their territories, but it is unknown what precipitated these events. The Richards pack moved north to a smaller portion of their original range, and the Dopp pack moved into the territory vacated by the Richards pack. These shifts constituted a dramatic change in range centres, and potentially pack membership. While territory shifts such as these are more typical of colonizing or recolonizing wolves (Fuller et al. 2003), wolves may also eliminate a neighbouring pack or create new territories as wolf populations fluctuate (Meier et al. 1995). Coincidentally, both the Dopp and Richards packs experienced den failure and high human-caused mortality prior to the shifts in range use.

Sizes of seasonal range use by wolves in the BP were related to respective movement rates during the winter, late winter, and denning seasons. Movement rates during the winter and late winter seasons were at a minimum, probably reflecting snow conditions and the

typical energy-minimizing strategy of straight, linear movements (Mech and Boitani 2003). During the spring and summer months when pups were restricted to den and rendezvous sites, seasonal ranges were proportional to the relative per-wolf availability of conifer stands. This pattern is likely related to the lack of prey potential in these habitats and the importance of efficient hunting forays in other habitats where prey is likely to occur during pup-rearing. Movement rates during denning tended to peak across all packs, likely related to pack members having to leave the den to hunt, and subsequently return again to the den to feed and care for pups (Fuller et al. 2003). Wolf movements within a territory have been found to differ between the pup-rearing season and the rest of the year (Mech 1970, Mech et al. 1998, Jedrzejewski et al. 2001). Once pups are fully grown, the pack is able to move as a nomadic unit without the need for extensive hunting forays from a central location (Musiani et al. 1998, Jedrzejewski et al. 2001).

Movement rates for wolves were greater than those observed for grizzly bears in the BP, but lower than those reported in other wolf populations. Movement rates across seasons and packs in the BP averaged 3.2 km/6hr overall (range 1.2 km/6hr to nearly 10.2 km/6hr). Average travel rates were approximately 2.4 km/6hr during the winter months compared to 3.6 km/6hr during the summer months. It has been reported that wolves can sustain daily travel rates of 8-9 km/hr (Mech and Boitani 2003), thus travelling up to 54 km in a 6 hr period. When wolves are returning to the den, travel rates may exceed 10 km/hr (Mech 1994), potentially covering 60 km in a 6-hr period. During winter, movements consist of travelling long distances while hunting, making a kill, feeding, resting, local movements near the kill, leaving the kill, and then repeating the cycle. Mech (1970) reported that collectively, these activities may result in average movement rates of 2.4 km/hr (or 14.4 km/6hr). Presumably during the summer, wolves require less rest in the absence of snow and are able

to cover greater distances in shorter periods of time (Fuller et al. 2003). The lower travel rates observed in my study could be a function of the GPS fix interval of 6 hours that may mask patterns such as back-tracking. Shorter fix intervals, however, may inflate estimates of movement rate. Fix rates of >3 hours have been shown to mask circadian activity patterns of wolves in Alaska (Merrill and Mech 2003). As a result, I caution against making comparisons of absolute rates, and highlight that peaks in movement rates during the pup-rearing phase and dips in movement rates during the winter months are consistent with observations of movement patterns of wolves in general.

Summary

Grizzly bears in the BP showed a high fidelity to annual ranges, and tolerated high spatial overlap among individuals, typical of high-quality habitats. Grizzly bears used smaller ranges, and travelled at lower rates than wolves. The striking feature in the grizzly bear models was the consistent inverse relationship between range size and the extent of *Elymus* burns across annual and seasonal ranges. This habitat class is reflective of young regenerating disturbance regimes, including both natural and prescribed fires designed to promote elk and Stone's sheep populations in the BP, as well as highly productive avalanche chutes. Although the importance of avalanche chutes and regenerating burns to grizzly bears has been well documented (e.g., Ramcharita 2000), I present a possible link between these habitats and home range size. These results are consistent with my observations of habitat use and selection within seasonal ranges (see Chapter 4). Among seasons, there was a significant reduction in space use and movement rates of females accompanied with cubs of the year compared with other family classes during spring and summer. These reductions may be related to security of cubs, as suggested elsewhere (e.g., Dahle and Swenson 2003a).

Wolves showed little overlap among packs, and the spacing of packs in natural systems may be as dynamic as populations colonizing more human-dominated landscapes. For wolves, annual and seasonal ranges were proportional to the extent of dense conifer stands, which may provide important cover habitat, particularly during denning, but which may be relatively poor in terms of ungulate prey availability. Both seasonal and annual range sizes also were directly proportional to low-productivity habitat (e.g., conifer), as indexed by NDVI, and pack size, which are linked to prey density (Fuller et al. 2003) and subsequently prey availability per wolf. As an obligate carnivore, the spatial distribution of wolves may be most impacted by the extent of space that will not support sufficient prey numbers. This contrasts with spatial use by grizzly bears that was inversely related to the extent of productive habitat where bears feed and may be sustained in the absence of ungulate prey. The extent of productive vegetative cover does not need to be as extensive to support grizzly bears, whereas wolves depend on mobile prey that are less predictable in their distribution.

My results taken together suggest that the spatial organization of territorial carnivores at the home-range scale may be driven by the relative productivity of available habitat classes reflective of plant biomass (for grizzly bears) and overall prey density. Movements within seasonal ranges may be a function of both habitat productivity related to foraging efficiency and security related to the rearing of young. Management directions should consider these hierarchical processes (e.g., McLoughlin et al. 2000; Ciarniello et al. 2007) and incorporate plans to maintain habitat opportunities that integrate long-term survival and fitness at the home-range scale with smaller scale processes that influence short-term nutritional and security requirements.

Chapter 3: Habitat Selection by Wolves (*Canis lupus*) in a Multi-Prey Ecosystem in the Northern Rocky Mountains of British Columbia.

Introduction

Wolf research in North America and Europe has focused primarily on prey selection (e.g., Mattioli et al. 1995; Okarma 1995; Forbes and Theberge 1996; Meriggi et al. 1996; Kohira and Rexstad 1997; Bergerud and Elliot 1998; Spaulding et al. 1998; Gade-Jørgensen and Stagegaard 2000; Jędrzejewski et al. 2000; Darimont et al. 2004; Smith et al. 2004); the estimation of kill rates (Hayes et al. 2000; Hebblewhite and Pletscher 2002; Hebblewhite et al. 2003; Smith et al. 2004); functional responses (Dale et al. 1994; Hayes and Harestad 2000b); the potential for wolves to limit and/or regulate prey populations (Eberhardt et al. 2003), particularly single prey systems (e.g., elk; Hebblewhite et al. 2002); impacts on ungulate population dynamics associated with wolf predation risk (Hebblewhite 2006; Hebblewhite and Merrill 2007); and the ability of wolves to structure entire communities by mediating trophic cascades (Ripple and Beschta 2004; Hebblewhite et al. 2005). Because public attitudes towards wolves have changed drastically in recent years in both Europe (Promberger and Schröder 1993) and North America (Kellert et al. 1996), numerous scientific modeling efforts have examined habitat use by wolves in human-dominated landscapes and predicted potential areas that may be suitable for wolf restoration and recolonization (Mladenoff et al. 1995, 1997; Haight et al. 1997; Massolo and Meriggi 1998; Mladenoff and Sickley 1998; Corsi et al. 1999; Mladenoff et al. 1999; Glenz et al. 2001; Apollonio et al. 2004; Cayuela 2004; Jędrzejewski et al. 2004), but relatively few have examined habitat use by wolves in relatively natural systems.

Wolves are habitat generalists (Mech 1995). Two critical habitat components for wolves are typically low human disturbance or human-caused mortality (typically indexed by road density) and an abundant supply of ungulates (Fritts et al. 1994). More specific habitat requirements of wolves in alpine or boreal systems may include elevated forested areas near water for denning, and meadows or semi-open to partially treed areas for rendezvous sites (Arjo and Pletscher 2004). Interspecific interactions, ease of travel, and energy requirements can also influence habitat use (Arjo and Pletscher 2004). In human-dominated landscapes in North America, favorable wolf habitat has been correlated most often with forest cover that included some conifer component, avoidance of agricultural land, and low road and human density (Thiel 1985; Mech et al. 1988; Mladenoff et al. 1995; Conway 1996).

In recent years, Geographic Information Systems (GIS) and remote sensing technology, in combination with various multivariate and regression procedures, increasingly have been used in wildlife ecology studies. Habitat selection is a hierarchical process (Johnson 1980). Studies on wolves using GIS generally focus on a coarse grain with the intent of projecting favorable wolf habitat and potential population recovery over regional scales (e.g., Mladenoff et al. 1995; Mladenoff and Sickley 1998; Glenz et al. 2001). At the coarse-grain scale of second-order selection (Johnson 1980), factors involved in selecting a home range may be difficult to quantify because of interactions with neighbouring packs, long-term trends in prey abundance and diversity, and how one defines the extent of the study area that is available for a home range. Use of finer grains can elucidate spatial and temporal variation in habitat selection strategies that may be occurring at smaller scales (e.g., Johnson et al. 2002a,b; Gustine 2005) and may be relevant to individual fitness (Rettie and Messier 2000).

I used logistic regression and resource selection functions with model inputs based on GIS and remote sensing, and global positioning systems (GPS) telemetry to model habitat selection by wolves in an intact large-mammal multi-prey system in the northern Rocky Mountains of British Columbia. I present data on selection within the home range based on analyses of fine-grain satellite imagery. I examined seasonal variation in habitat selection and how strategies differed among packs. I also compared the importance of 1) habitat class, 2) vegetation biomass or quality, and 3) relative selection values for particular prey species in the best predictive models of habitat selection by wolves.

I was interested in examining the ecology of a resident wolf population in a relatively natural system rather than looking at broad patterns of habitat occupancy (e.g., Mladenoff et al. 1999). Chapter 2 established the framework for this analysis by providing information on the amount of space used by wolves, and discussed potential variables that explain the variation in these patterns. The initial discussion on home ranges introduced constraints to resources that are available to each pack. The spatial distribution of wolf packs, and how wolves use vegetation classes and physiographic features within home ranges, determine energy expenditures and prey encounter rates that influence ecosystem dynamics. The analyses for wolves presented in the chapter were conducted concurrently with resource selection studies of grizzly bears (see Chapter 4). Comparisons of resource use between wolves and grizzly bears provide insight into the overall functioning of this large-mammal predator-prey system. Analyses of resource selection logically lead to an examination of prey consumption (see Chapter 5) to validate or refute species interactions as inferred by the use of habitat classes, and the potential relationships with prey interactions.

Methods

Study Area

The 6.4 million-ha Muskwa-Kechika Management Area (MKMA) in northeastern British Columbia was established as a special area owing to its relatively large size and unroaded expanse, as well as its cultural, ecological, and geographical diversity. Management designations within the area include wilderness conservation areas and parks set aside to protect sensitive areas and wildlife, and regions designated as special management zones where some level of resource development is permitted and encouraged, bearing in mind the need to balance other land values. My research occurred in the Besa-Prophet study area (BP), which includes the 204,245-ha Besa-Prophet pre-tenure planning area (a zone managed for oil and gas exploration and development in the southeastern portion of the MKMA), the 80,771-ha Redfern-Keily Provincial Park adjacent to and southwest of the Besa-Prophet pre-tenure planning area, and portions of surrounding areas. The topography is characterized by wide, prominent east-west river valleys with their headwater systems located in rugged high-mountain terrain in the western extent of the study area where elevations can exceed 3000 m. A series of north-south ridges, with elevations generally below 2500 m, characterize the central portion of the study area that features rolling topography typical of foothills-type terrain. The eastern portion of the study area is bounded by an expanse of open spruce flats and muskeg habitat with patches of upland aspen (*Populus tremuloides*) stands. The BP supports one of the largest intact predator-prey ecosystems in North America. Ungulates include moose (*Alces alces*), elk (*Cervus elaphus*), caribou (*Rangifer tarandus*), Stone's sheep (*Ovis dalli stonei*), and mountain goats (*Oreamnos americanus*). Numerous predators can be found in the region, but only wolves and grizzly

bears (*Ursus arctos*) are of sufficient number to be capable of limiting or regulating ungulate communities.

The study area is dominated by 2 biogeoclimatic zones (Meidinger and Pojar 1991): the spruce-willow-birch (SWB) zone of sub-alpine spruce, willow (*Salix sp.*), and birch (*Betula glandulosa*), and alpine tundra (AT) at elevations >1600 m. The SWB zone in the BP occupies elevations ranging between 800 and 1600 m. Valleys in the SWB zone consist of intermittent to closed forest cover of white spruce (*Picea glauca*) and variable amounts of lodgepole pine (*Pinus contorta*) and aspen in the valley bottoms and on lower slopes. The AT zone, comprising approximately 16% of the BP, is treeless, unless trees are in stunted or krummholz form. Alpine vegetation is dominated by a dwarf scrub of prostrate woody plants and some herbs, bryophytes, and lichens, but much of the alpine landscape consists of rock, ice, and snow. In the BP, *Dryas spp.* and *Cassiope spp.* are the dominant dwarf scrub vegetation in this zone.

Wolf Capture and Locational Data

Twenty-six wolves from 5 packs (Pocketknife, Lower Besa, Nevis, Dopp, Richards) were monitored with GPS collars (Simplex-Televilt, Lindesberg, Sweden) between December 2001 and September 2004. Following den failure in 2002, both the Dopp and Richards packs shifted their territories and pack membership in 2003 and were renamed the Keily and Prophet packs respectively. I programmed collars to acquire locations every 6 hr for 2 years. At least 2 and up to 4 collars were deployed in a pack at any given time to account for the possibility of collar failure and dispersal. I retrieved GPS data via remote download or collar retrieval. Locations obtained on the day of capture and 24 hr after capture were not included in analyses. Given the social structure of wolves, selection herein was

analyzed at the pack level (Type III design, Thomas and Taylor 1990, 2006) within a home range (3^{rd}-order selection, Johnson 1980). To avoid pseudoreplication, only one randomly chosen location from a set of duplicate locations obtained at the same date and time from multiple collars was kept for analysis.

Study Design

Telemetry locations were used to estimate resource use, and compared to randomly sampled locations using logistic regression (Manly et al. 1993, Boyce and MacDonald 1999). I defined availability as all areas within 95 % annual minimum convex polygon (MCP) home ranges. I assumed that locations near the periphery of a home range were related to territory marking or potentially other forays not related to core habitat use, and so the effect of extra-territorial movements and potential pre-dispersal forays was removed by using only 95 % of locations closest to the range centre of each wolf pack (e.g., Bowen 1982). To characterize availability, 5 availability points per use point (e.g., Gustine et al. 2006) were randomly generated within each annual MCP for each pack, year, and season using the random point generator extension (Jenness 2003) in Arcview 3.2. I identified 5 seasons for wolves based on biological criteria: winter (1 January to 28 February, breeding and peak snow depth), late winter (1 March to 31 April, pre-denning activities), denning (1 May to 31 July, pup-rearing and ungulate calving), late summer (1 August to 31 September, nursery stage when pups are physically immature and nurse at rendezvous sites), Fall (1 October to 31 December, pups are nearly fully grown and traveling with the pack). For a season to be included in analyses and satisfy issues of sample size and model separability, I set 50 use points as a minimum for that season. Coefficients from logistic regression analyses were used to define habitat selection by year and season across wolf packs (global) and within wolf packs.

GIS and Remote Sensing Data

Vegetative and topographical covariates in resource selection model sets for wolves were 25-m resolution raster GIS data. Elevation was extracted from a digital elevation model (DEM, 1:20,000 British Columbia Terrain and Resource Inventory Management program, 1996), which also was used to create slope and aspect layers (Gustine 2005). Aspect was categorized into north (315-45°), east (45-135°), south (135-225°), and west (225-315°) directions. Pixels with slope $\leq 1°$ were assigned no aspect (NAS). Elevation (km) and slope (°) were entered as quadratic in all selection models. Fifteen vegetation classes were identified using an August 2001 Landsat Enhanced Thematic Mapper 7 image (Lay 2005) and then combined into 10 major habitat classes according to similarity of vegetation and elevation and possible prey associations (e.g., moose and riparian spruce; elk and deciduous burns; caribou and open alpine; sheep and *Elymus* burns) (Table 3.1). An index of vegetation fragmentation was created from the initial vegetation classes, which were grouped according to coarse vegetation cover to represent fragmentation as open or closed cover types (Gustine 2005). Fragmentation was grouped into 3 classes (low, medium, and high), and used as an index of habitat diversity. Categorical classes for which there was no use were omitted from the models. Numerous studies have found the seasonal differences in multi-temporal Normalized Difference Vegetation Index (NDVI) values to be important in explaining movements of wildlife species (Lay 2005). NDVI is correlated with plant biomass (Tucker and Sellers 1986; Ruimy et al. 1994) and the change in NDVI is correlated with vegetation quality (Oindo 2002). Lay (2005) used 14 Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) images from Landsat satellites to generate NDVI images at 25-m

Table 3.1. Habitat classes (and their respective vegetation associations) used in analyzing habitat selection by wolves in the Besa-Prophet study area of northern British Columbia.

Habitat classes	% of Study Area	Description
Conifer	22.3	Dense mid-elevation pine (*Pinus contorta*) and white and hybrid spruce (*Picea glauca, P. mariana x glauca*)-dominated forest stands.
Stunted Spruce	5.6	Open spruce areas typical of north-facing slopes.
Shrub	5.7	Willow (*Salix* spp.) and birch (*Betula glandulosa*) shrub communities ≤1600 m.
Alpine Shrub	5.7	Willow and birch shrub communities >1600 m.
Non-Vegetated	23.7	Rock (boulder, talus), rock-lichen associations, water, snow.
Riparian Spruce	17.7	Low elevation (<1600 m) wetland spruce (*P. glauca* or *P. mariana* in poorly drained sites) along streams; includes gravel bars and sedge (*Carex* spp.) meadows.
Open Alpine	5.5	Dry alpine tundra habitat >1600 m characterized by *Dryas* spp.; wet alpine tundra habitat >1600 m dominated by *Cassiope* spp. and sedge (*Carex* spp.) meadows.
Deciduous Burns	7.1	Older burns; characterized by deciduous shrubs and regenerating young aspen/poplar (*Populus tremuloides* and *P. balsamifera*) stands.
Elymus Burns	3.2	Younger burns; meadows dominated by *Elymus innovatus*.
Sub-alpine Spruce	3.5	Open spruce; transition zone between dense mid-elevation spruce stands and open alpine areas.

resolution during the growing season for 3 years (2001-2003) in my study area. I used these NDVI and change in NDVI values and substituted them for the habitat classification in competing models to determine whether habitat class or habitat productivity/quality, as potentially related to the distribution of ungulate prey, was important in driving selection patterns of wolves. I was able to analyze NDVI in selection models only for the denning and late summer seasons.

Concurrent with this study, GPS data were collected on the movements of prey and used to generate relative selection layers by season for moose (Gillingham and Parker 2008a,b), elk (Heinemeyer et al. 2004a,b), Stone's sheep (Walker 2005, 2007), and caribou (Gustine 2005). Combinations of these layers were incorporated as models competing with those generated from habitat class and landscape features to determine the extent to which high selection values for prey may contribute to the habitat selection patterns of wolves. The final models used to generate these layers are presented in Appendix B, Table B1.

Modelling Procedures

I used the information-theoretic approach to evaluate selection models (Burnham and Anderson 2002). I constructed global models across years and packs by pooling GPS locations, and seasonal selection models. Categorical variables were coded with deviation contrasts (Menard 2002). To avoid inflating selection coefficients and associated standard errors (Menard 2002), I assessed collinearity among habitat variables. Given the high number of parameters in my model sets and the number of models generated, I used a conservative tolerance score of < 0.3 to assess potential collinearity (Sokal and Rohlf 2000). Correlated variables were substituted in identical models and ranked separately. For example, vegetation biomass (NDVI), vegetation quality (change in NDVI), and an

interaction term (biomass x quality) were entered as separate covariates in competing models given the high degree of collinearity (tolerance < 0.3) among variables. A list of all candidate models is provided in Appendix B, Table B2.

I used Akaike's Information Criterion (AIC_c) corrected for small sample sizes ($n/K < 40$) to rank the model sets for wolf packs. The differences in AICc (Δ_i) provide an estimate of the distance that a candidate model is from the true model (Burnham and Anderson 2002). Akaike's weights (w_i) provide an estimate of the relative probability that the top model is the best amongst the suite of candidate models. I selected a single model as the likely top model if its w_i was ≥ 0.90. If the top model had an associated $w_i < 0.90$, I averaged the selection coefficients (β_i) from the suite of top candidate models for which the sum of their respective w_i's was ≥ 0.95 (Burnham and Anderson 2002). I used the k-fold cross-validation procedure averaged across 5 random subsets and a Spearman's rank correlation (r_s) to determine the predictive ability of each top model; values of $r_s > 0.70$ indicated good model performance (Boyce et al. 2002).

I also specifically analyzed use of different elevations because of the importance of this attribute to the distribution of other species in the BP. I compared mean elevations across seasons with one-way analysis of variance (ANOVA) across all wolves, where season was entered as a fixed effect, and at the pack level, where the combination of pack and season was examined as the fixed effect. I used Tukey's honestly significant difference (HSD) test for post-hoc comparisons. I assumed significance of all tests at $\alpha = 0.05$. All means are presented as $\bar{X} \pm 1$ SE unless noted otherwise.

Results

I retrieved 7,447 GPS locations from 25 collared wolves in 5 packs between December 2001 and September 2004. I observed a 61% ± 7% (mean ± SD; range = 52 to 70%) average fix rate across packs. Individual collars had high failure rates. These average fix rates were based on the total number of locations obtained per pack over the course of the study owing to the deployment of multiple collars per pack, after removing duplicate locations. Fix rates also were corrected by removing 24-hr periods during which a location was not obtained by a collar (D.C. Heard, BC Ministry of Environment, pers. comm.). A total of 499 collar-days were removed (approximately 16 % of the total sampling period).

Seasonal Use and Selection Across Wolves

Habitat Use

Depending on season wolves tended to use riparian spruce (use = 18 - 30 % of locations), shrub communities (14 - 25 %), and conifer stands (15 - 18 %) more than other habitat classes (Table 3.2). Use of alpine shrub communities increased from <6 % in the winter and late winter to 10 - 15 % between denning and fall. Approximately 30 - 50 % of all wolf locations were in forested cover types (conifer, stunted spruce, riparian spruce) across seasons. On average, the least used of the habitat classes were stunted spruce (3 - 7 %), non-vegetated (2 - 6 %), open alpine (3 - 8 %), and sub-alpine spruce (2 - 6 %). Wolves used the burned habitat classes most during the late winter (~20 % total), compared to other seasons (4 - 12 %).

East aspects were the most consistently used (22 - 28%) landscape features, whereas west (10 - 16 %) and flat areas (9 - 12 %) were used least (Table 3.3). Use of south aspects ranged from a low of 20 % in late summer to a high of 37 % in late winter, which

Table 3.2. Summary of % relative use (U) versus availability (A) of habitat classes by radio-collared wolves in the Besa-Prophet study area of northern British Columbia. The summary is based on pooled GPS locations between 2001 and 2004. Seasons are Winter (W), Late Winter (LW), Denning (D), Late Summer (LS), Fall (F). Veg. = Vegetated, Decid. = Deciduous.

Pack	Season[a]	N	Conifer		Stunt		Shrub		Alpine Shrub		Non-Veg.		Riparian		Open Alpine		Decid. Burns		*Elymus* Burns		Sub-Alpine Spruce	
			U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A
Global	W	980	15	25	5	6	24	6	6	8	5	17	22	17	6	8	6	7	6	3	4	4
	LW	1847	17	24	7	6	14	6	3	9	6	21	27	13	4	8	11	6	9	3	2	4
	D	2142	18	23	3	6	19	6	11	9	5	22	30	13	4	8	4	6	3	3	4	4
	LS	1067	17	25	3	7	21	6	13	8	2	19	29	13	7	8	3	8	1	3	4	4
	F	1411	15	24	3	6	22	6	14	9	5	21	18	13	8	8	8	6	2	3	6	4
Pocket-Knife	W	242	17	30	5	7	17	6	0	0	0	4	47	41	3	3	6	7	5	2	0	0
	LW	277	14	31	4	7	17	6	0	0	2	3	53	40	3	3	4	7	3	3	0	1
	D	333	14	29	4	7	13	7	0	0	1	2	62	42	0	3	5	6	1	2	0	1
	LS	193	15	33	3	7	16	7	3	0	1	2	50	37	9	3	3	7	1	3	0	1
	F	199	19	30	3	7	12	6	1	1	1	4	42	42	12	2	8	7	2	3	1	0
Lower-Besa	W	134	16	27	12	11	19	7	1	2	4	8	34	18	1	6	10	14	4	5	0	2
	LW	293	13	26	7	12	11	6	1	2	4	10	34	18	1	4	19	14	10	5	0	2
	D	306	11	26	7	12	16	7	0	2	1	9	57	17	0	5	5	14	2	5	1	3
	LS	221	19	23	7	12	12	6	0	2	1	11	49	19	1	5	9	14	1	6	1	2
	F	245	22	28	7	13	23	5	1	2	3	7	23	19	2	4	16	13	2	6	2	3
Nevis	W	288	13	31	3	4	41	9	7	11	4	12	6	7	10	10	7	6	3	3	5	7
	LW	469	15	32	9	5	22	10	4	11	4	8	15	7	7	11	9	6	11	3	4	7
	D	471	22	31	1	5	45	9	8	11	4	10	14	7	2	11	1	6	1	3	2	7

Table 3.2 Continued

Pack	Season[a]	N	Conifer		Stunt		Shrub		Alpine Shrub		Non-Veg.		Riparian		Open Alpine		Decid. Burns		*Elymus* Burns		Sub-Alpine Spruce	
			U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A
Nevis	LS	299	20	31	1	6	41	10	12	12	1	10	11	6	8	11	1	6	0	3	4	6
	F	404	12	31	3	5	40	10	9	12	3	8	12	7	7	12	7	6	2	4	6	6
Richards[b]	LW	146	12	15	18	4	15	5	1	12	6	42	26	5	3	8	5	4	12	2	1	4
	D	260	15	16	4	4	13	3	13	12	8	42	25	4	7	10	4	3	5	2	7	4
	LS	126	14	16	1	4	17	3	13	11	8	43	32	4	4	9	2	4	2	1	7	6
	F	240	7	16	1	3	11	4	30	11	15	42	8	5	11	9	4	4	4	2	8	5
Prophet	W	221	16	13	5	2	21	3	6	13	9	44	16	6	5	10	5	3	10	2	7	5
	LW	279	11	12	4	2	13	4	6	13	10	43	32	5	3	11	7	2	13	2	2	5
	D	317	10	10	2	3	16	4	23	14	9	44	15	5	8	10	5	3	7	3	4	5
	F	170	14	11	1	2	10	4	36	16	5	43	15	5	7	11	4	2	3	2	6	4
Dopp[b]	LW	207	30	20	9	3	2	4	7	10	9	38	15	8	6	7	15	4	4	1	2	5
	D	234	24	20	1	3	4	4	15	9	8	39	23	9	6	6	6	4	4	1	9	5
	LS	147	21	21	0	3	7	3	35	9	3	37	14	7	10	7	1	6	1	2	8	5
	F	153	22	19	2	3	14	4	18	10	5	38	11	7	7	7	5	4	3	1	12	6
Keily	W	95	15	24	5	6	7	3	21	13	7	21	7	5	15	13	2	6	6	3	14	6
	LW	176	32	19	3	6	8	4	4	15	3	24	18	7	3	10	15	4	9	3	6	6
	D	221	38	24	5	6	4	3	23	15	3	25	14	7	3	9	4	4	1	3	5	5

[a] W = 1 January - 28 February, LW = 1 March - 31 April, D = 1 May - 31 July, LS = 1 August - 30 September, F = 1 October - 31 December.

[b] The Dopp and Richards packs were followed throughout 2002, but both packs shifted their territories during 2003 and were renamed the Keily and Prophet packs respectively. The range centres were sufficiently different to warrant separate analyses.

Table 3.3. Summary of the relative use (%) of landscape features by wolves in the Besa-Prophet study area of northern British Columbia. The summary is based on pooled GPS location data between 2001 and 2004. NAS = No Aspect (< 1° slope).

			Aspect					Fragmentation[b]		
Pack	**Season[a]**	***N***	**N**	**E**	**S**	**W**	**NAS**	**Low**	**Med**	**High**
Global	Winter	980	23	25	29	13	9	15	34	51
	Late Winter	1847	15	23	37	16	9	15	33	51
	Denning	2142	26	22	29	10	12	18	34	48
	L. Summer	1067	28	28	20	14	11	17	35	48
	Fall	1411	26	28	25	13	8	19	36	45
Pocket-Knife	Winter	242	22	38	18	7	15	15	33	52
	L. Winter	277	20	27	17	14	21	13	37	50
	Denning	333	25	32	11	8	24	16	39	45
	L. Summer	193	23	36	22	10	9	12	30	58
	Fall	199	29	34	16	13	10	12	37	52
Lower-Besa	Winter	134	28	28	12	16	15	13	31	55
	L. Winter	293	13	23	43	12	10	18	27	56
	Denning	306	18	25	21	18	19	7	26	67
	L. Summer	221	26	29	14	12	19	11	29	60
	Fall	245	29	32	18	10	11	19	35	46
Dopp	L. Winter	207	14	18	40	23	5	12	42	47
	Denning	234	19	19	46	4	13	17	31	52
	L. Summer	147	27	32	28	7	6	22	37	41
	Fall	153	16	25	38	14	7	16	30	54
Keily	Winter	95	23	22	43	8	3	18	37	45
	L. Winter	176	12	22	52	7	7	19	27	55
	Denning	221	16	20	48	8	7	26	44	30
Richards	L. Winter	146	19	10	40	25	7	14	33	53
	Denning	260	27	24	33	7	9	22	32	47
	L. Summer	126	22	25	25	16	12	18	33	49
	Fall	240	31	22	28	17	1	29	32	39
Prophet	Winter	221	29	18	33	13	7	10	31	60
	L. Winter	279	14	24	39	15	8	15	34	51
	Denning	317	21	25	35	14	6	19	30	51
	Fall	170	26	31	25	12	6	16	35	49
Nevis	Winter	288	18	20	40	16	6	20	38	42
	L. Winter	469	16	25	37	16	6	16	33	51
	Denning	471	42	14	25	10	8	23	37	40
	L. Summer	299	36	20	17	17	9	20	41	39
	Fall	404	25	25	27	13	11	21	40	39

[a] Winter = 1 January - 28 February, (L)ate Winter = 1 March - 31 April, Denning = 1 May - 31 July, (L)ate Summer = 1 August - 30 September, Fall = 1 October - 31 December.
[b] Fragmentation is an index of vegetative diversity (see text).

corresponded with the lowest use of north aspects in late winter (15 %). Aside from late winter, the use of north aspects was fairly consistent (23 - 28 %). Approximately half of all wolf locations were in high fragmentation areas across seasons, and <20 % were in low fragmentation areas.

Mean elevations used by all wolves varied between 1,280 and 1,400 m depending on season (range = 664 - 2,401 m) and were significantly different across seasons ($F(4,7442) = 39.01$, $P < 0.0001$) (Figure 3.1). Wolves used elevations that were significantly lower during the late winter season than during other times of the year ($\overline{X}$: 1,286 m, range: 724 - 2,250 m). The highest elevations were used during fall ($\overline{X}$: 1,399 m. range: 771 - 2,177 m).

Seasonal Selection Strategies

Habitat class, fragmentation, aspect, slope, and elevation were attributes in all of the top selection models (Appendix B, Table B3). Wolves responded to elevation during the winter and late winter seasons, whereas slope was included in the models for wolves during the denning, late summer, and fall seasons. Model performance, as measured by Spearman's rank correlation, was high ($r_s = 0.87$ to 0.99).

Specific vegetation and landscape features were consistently selected or avoided by wolves in the BP (Tables 3.4, 3.5). Wolves tended to avoid conifer stands, stunted spruce areas, non-vegetated areas, low-fragmentation areas, and west aspects year-round. Wolves selected for shrub communities and high-fragmentation areas across seasons. Other habitat classes were seasonally important to wolves. Wolves selected alpine shrub communities during denning, late summer, and fall; *Elymus*-dominated burns during winter, late winter, and denning; sub-alpine spruce during late summer and fall (avoided during late winter);

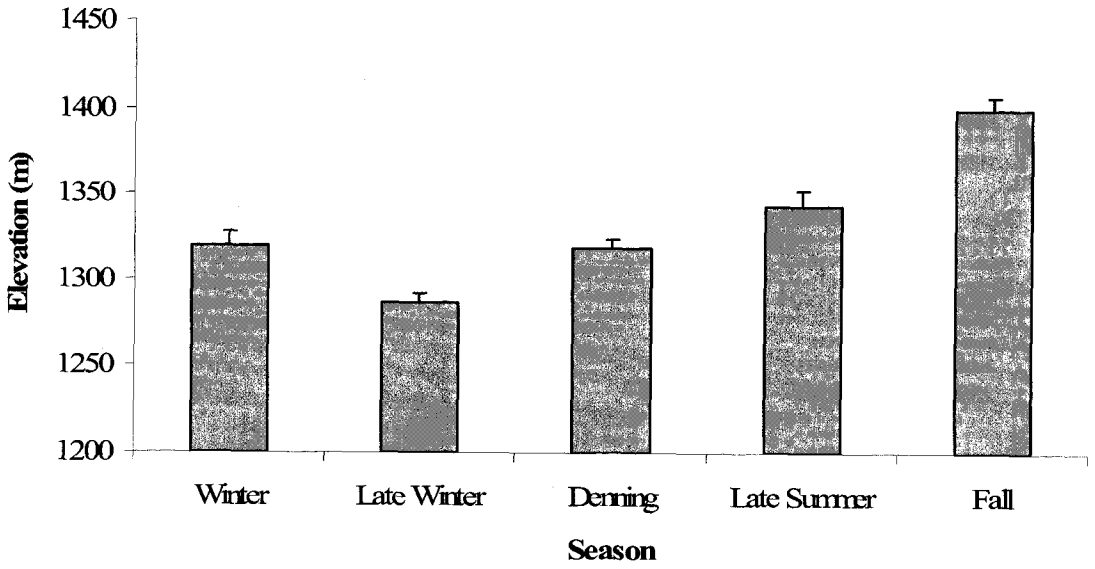

Figure 3.1. Global seasonal mean (± *SE*) elevations used by wolves in the Besa-Prophet study area of northern British Columbia, 2001-2004. Winter $n = 980$, Late Winter $n = 1847$, Denning $n = 2142$, Late Summer $n = 1067$, Fall $n = 1411$.

and open alpine areas during winter, late winter, and late summer (avoided during denning). North aspects were avoided by wolves during the later winter months, but selected from denning through fall. South aspects were also seasonally important as wolves selected for these areas during later winter and denning. None of the top-ranked models describing habitat selection by wolves included prey selection value or vegetation biomass (NDVI) or quality (change in NDVI).

Seasonal Use and Selection by Individual Wolf Packs

Habitat Use

Individual wolf packs were variable in their use of habitat classes across seasons (Table 3.2). The Lower Besa and Pocketknife pack were found primarily in riparian spruce areas (23 - 63 %) year round. The reduction in use of riparian spruce by the Lower Besa pack during the fall was associated with a corresponding increase in the use of shrub communities (23 %) and deciduous burns (16 %). Shrub communities (11 - 23 %) and conifer stands (11 - 22 %) were also heavily used by these 2 packs. In contrast, the Nevis pack appeared to concentrate its activities in shrub communities (22 - 45 %), followed by conifer (12 - 22 %) and riparian spruce (6 - 15 %) areas. During 2002, the Dopp pack was found primarily in conifer stands (21 - 30 %) and riparian spruce (11 - 23 %), but also showed a marked increase in their use of alpine shrub communities between denning and fall (14 - 35 %). When the Dopp pack shifted its territory to become the Keily pack in 2003, conifer stands were still frequented (14 - 38 %) as were alpine shrub (4 - 23 %) and riparian spruce (7 - 18 %) communities during the 3 seasons for which data were available. Similarly, the Richards pack in 2002 increased their use of alpine shrub between denning and fall (13 - 30 %). This pattern was consistent in 2003 when the pack shifted its territory

to become the Prophet pack, and increased its use of alpine shrub from an average of 6 % during winter and late winter to 21 - 30 % between denning and fall. Both these packs also made significant use of riparian spruce (Richards: 8 – 32 %; Prophet: 15 – 32 %) and shrub (Richards: 11 - 17 %; Prophet: 10 - 21 %) communities. All packs, with the exception of the Pocketknife pack, appeared to increase their use of burned community types (18 - 29 %) during the late winter season.

Individual wolf packs varied in their use of aspect and slope on the landscape (Table 3.3). The Pocketknife and Lower Besa packs appeared to use east (23 - 37 %) and north (13 - 29 %) aspects most. Fewer than 22 % of the locations for these 2 packs throughout the year, with the exception of the Lower Besa pack in late winter (43 %), were on south aspects. In contrast, south aspects (17 - 52 %) were heavily used by the other 5 packs year-round, followed by north (14 - 42 %) and east (10 - 32 %) aspects. Pocketknife and Lower Besa packs also used flat areas (9 - 24 %) more than other packs (<13 %). Across packs, high fragmentation (30 - 67 %) areas were used more frequently than low (7 - 29 %) or medium (27 - 44 %) fragmentation areas.

Across seasons, wolf packs differed in their elevational distribution ($F_{(31,7415)}$, $P < 0.001$). Both the Pocketknife and Lower Besa packs, which occupy the boreal flats at the eastern portion of the study area, used significantly lower elevations than the other packs year-round with elevations consistently below 1,200 m (Figure 3.2). For these packs the lowest mean elevations were during denning ($\overline{X}$ ± SE; Pocketknife: 1,061 ± 9 m, Lower Besa: 976 ± 9 m). The other packs used lowest elevations during the late winter season ($\overline{X}$ ± SE; Nevis: 1,389 ± 9 m; Richards: 1,258 ± 14 m; Prophet: 1,315 ± 13 m; Dopp: 1,445 ± 13 m; Keily: 1,393 ± 13 m). Wolves were more variable in their distribution at higher

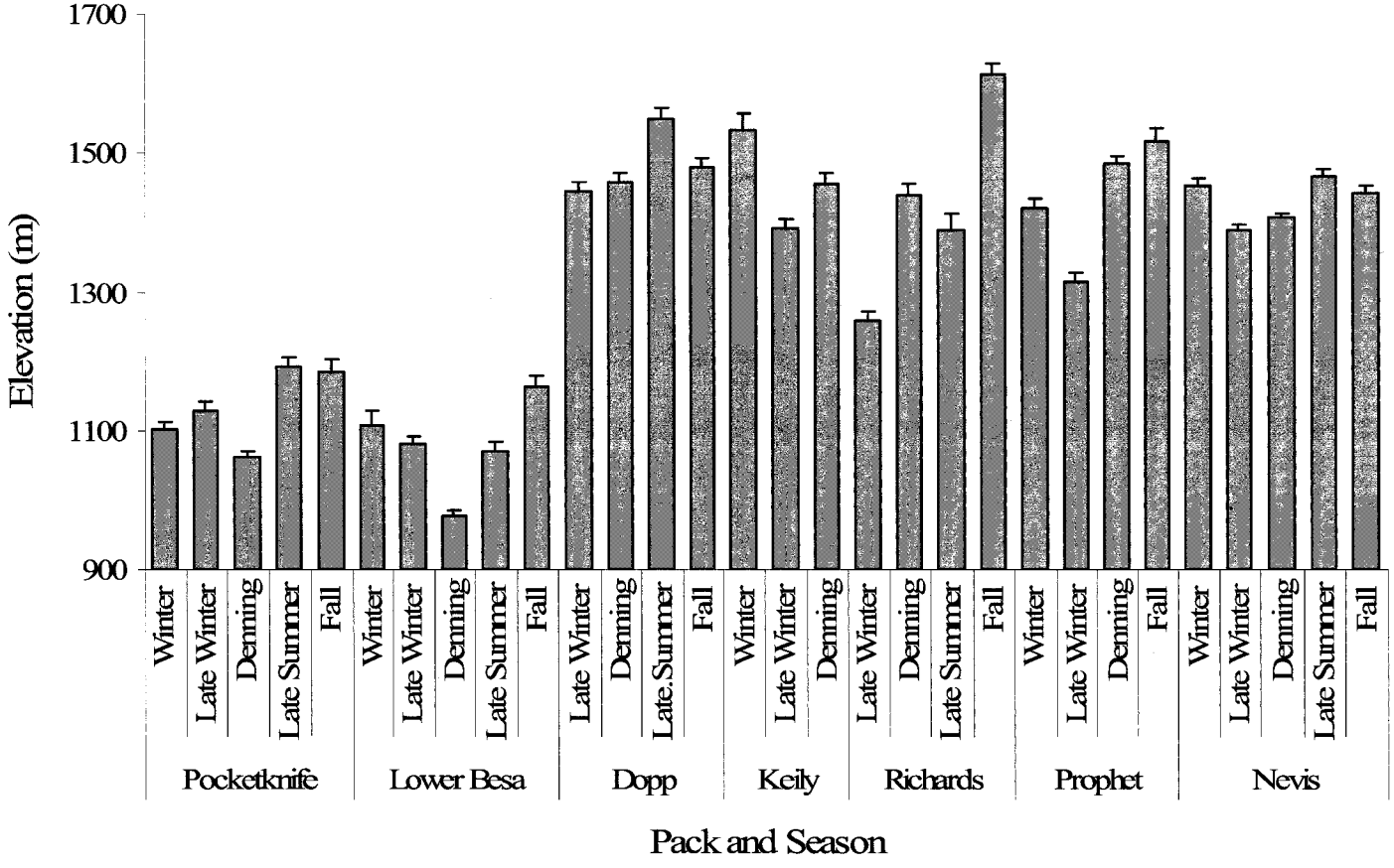

Figure 3.2. Seasonal variation in mean elevations (± *SE*) used by wolf packs in the Besa-Prophet study area of northern British Columbia, 2001-2004. Data were not available for the Dopp and Richards packs in winter, Keily pack in late summer and fall, and Prophet in late summer.

elevations across the other seasons, with the Richards pack found at the highest mean elevation during fall (1,613 ± 30m).

Habitat Selection

I pooled seasonal data across years for each season because few collars yielded >2 years of data for a particular season. With 4 exceptions (variables associated with NDVI and prey distribution), habitat class was prevalent in all top-ranked models across seasons for all packs (Appendix B, Table B4, n = 30 pack by season combinations). Additional variables included aspect (16/30 cases), fragmentation (11/30), elevation (16/30 cases), and slope (13/30 cases). Averaging was required in all but 4 models, with the number of models in an average set per pack ranging from 2 to 6. In 18 of the 26 seasonal models that required averaging, the top model had a weight (w_i) greater than twice that of the second ranked model. Model performance as estimated by Spearman's rank correlation (r_s) was good overall. Only 2 top-ranked models yielded an $r_s < 0.70$. In general, models describing winter selection by individual wolf packs had the poorest fit.

Various habitat classes were selected seasonally by wolf packs in the BP (Table 3.4). All packs tended to avoid conifer stands and non-vegetated areas (athough coefficients often were not significant in the models). The Nevis pack selected for shrub communities year round, but this habitat class was selected by the other packs in less than half the seasons. The Dopp pack appeared to specialize in alpine environments where it selected for alpine shrub and open alpine habitat classes between the denning and fall seasons during 2002, and again in the winter of 2003 when it shifted its territory as the Keily pack. Habitat biomass, as indexed by NDVI, was only used in model analyses during the denning and late summer seasons. Habitat biomass was included only in 4 top-ranked models, and was significant in

only 2 of those models. The Pocketknife (β = -2.85 ± 0.48) and Lower Besa (β = -1.63 ± 0.36) packs both selected against high biomass areas during denning. Only the Richards pack responded directly to the relative habitat quality for prey. The pack selected for areas ranked as potentially high quality for moose during the denning (β = 0.74 ± 0.31) and fall seasons (β = 5.46 ± 0.33) and avoided areas of potentially high quality for caribou (β = -0.61 ± 0.26) during denning and for elk (β = -3.08 ± 0.24) and Stone's sheep (β = -0.64 ± 0.31) during the fall.

Even fewer consistent patterns emerged in the selection of landscape features by wolf packs in the BP (Table 3.5). For example, the Lower Besa, Pocketknife, and Prophet packs selected for high fragmentation areas in 3 of the 5 seasons, but the Nevis pack avoided these areas during the fall. North aspects were generally associated with negative coefficients, with the exception of the Nevis pack that selected for north aspects from denning through fall. Selection models for all packs except the Pocketknife included positive coefficients for south aspects in late winter and denning, although many of these coefficients were not significant.

Discussion

With increasing rates of human development and subsequent habitat fragmentation, the opportunity to examine habitat selection by large carnivores in relatively non-impacted systems is increasingly uncommon. I examined habitat selection by a previously unstudied wolf population in an intact predator-prey ecosystem in the northern Rocky Mountains of British Columbia where future oil and gas development is likely to occur. Human disturbance in the region is currently limited to hunting and trapping, and a lightly used

ATV trail that crosses the southern portion of the study area through the territory of the Nevis pack. Most wolf studies have been concerned with occupancy, i.e., predicting where wolves will occur by identifying suitable habitat on the landscape for future colonization based on where wolves currently reside (e.g., Mladenoff et al. 1995, 1999; Mladenoff and Sickley 1998; Carroll et al. 2003; Gehring and Potter 2005; Potvin et al. 2005; Oakleaf et al. 2006). In contrast, I examined the activities and dynamics of a resident wolf population that is currently free of human disturbance. I demonstrated that wolves in the BP are responding to habitats within their home ranges. Such information may have important implications to the long-term management and persistence of this wolf population, and guide future studies in other regions.

Habitat selection by animals is a hierarchical process (Johnson 1980). An organism first selects a home range (2^{nd}-order selection) and then selects habitats within that home range (3^{rd}-order selection) that satisfy nutritional, thermal, and security requirements (Johnson 1980). Wolf occupancy is generally dependant on overall prey density and minimal human disturbance (Fritts et al. 1994); the establishment of a territory by a pack is subsequently dependent on the distribution of neighbouring packs, and its ability to defend its boundaries. Habitat selection may be seen as scale-dependent if contributions to reproductive fitness differ at different levels of selection (Orians and Wittenberger 1991; Schaefer and Messier 1995; Rettie and Messier 2000; McLoughlin et al. 2004). To optimize fitness, a wolf pack needs to use its range efficiently to minimize energy expenditures and maximize prey encounter rates (Alexander et al. 2005). In addition, while excluding conspecifics, wolves may need to use their home range in a manner that partitions prey resources, either spatially or temporally, to enable coexistence with other sympatric

predators (Husseman et al. 2003; Alexander et al. 2006; Garneau et al. 2007). These factors should be reflected in patterns of fine-scale habitat selection that can be used in managing for resource development. Processes within home ranges have largely been ignored in ecological studies of wolves, partly because of their designation as habitat generalists and partly because of general conclusions from broad-scale studies that relate wolf occupancy of a landscape to prey density (Fuller 1989; Messier 1995; Potvin et al. 2005) and road density (Mladenoff et al. 1995). As a result, wolf management has largely taken the view that as long as prey densities are sufficient to support wolf populations and as long as road densities (as an index of human-caused mortality) remain below a threshold of 0.58 km/km^2 (Thiel 1985; Fuller 1989; sic Carroll et al. 2000), wolves will persist. Even though wolves occupy a wide variety of habitats, however, they may still show affinity at finer scales, such that selection value for wolves could be expected to change within a regional landscape (Ciucci et al. 2003).

I did not examine 1st and 2nd order selection because in the alpine environment of the BP where habitats for denning and rendezvous sites are probably not limiting, where there are no roads, and where there are high non-migratory ungulate densities, wolf occupancy is virtually assured. Distribution most likely depends on intra-specific competition and subsequent spacing, and niche differentiation with other sympatric carnivores, such as grizzly bears. There is a need in carnivore research to understand how species select resources within their home range during different time periods and within different guild assemblages (Johnson et al. 1996; Arjo and Pletscher 2004). Few studies have addressed wolf habitat use at the home range scale, and fewer still that allow statistical inferences based on use versus availability of habitat resources (Thurber et al. 1994; Singleton 1995;

Paquet et. al 1996; Ciucci et al. 1997; Kunkel and Pletsher 2001; Ciucci et al. 2003). I focused my analyses on 3rd order selection processes of 5 individual wolf packs. The territories of these 5 packs sufficiently overlapped the extent of the Besa-Prophet pre-tenure planning area to consider these animals as the population for management. Management decisions should integrate, to the extent possible, the degree of variation amongst a population, particularly because the cumulative effects associated with large-scale developments may be non-linear and difficult to predict (Johnson et al. 2005). As development in the BP progresses predictably from east to west, the identification of seasonally important habitats across and within wolf packs should help to mitigate wide-sweeping impacts. In particular, it is unknown how impacts to 1 pack may cascade across neighbouring packs, as well as other wildlife distributions. Given the sudden shifts in territory boundaries of 2 packs in the BP, it is apparent that wolves may be sensitive to moderate levels of human disturbance and the condition of neighbouring packs.

Collectively, wolves in the BP appeared to respond to habitat class. Vegetation associations are indicative of prey habitat (Carroll et al. 2000; Swan 2005). The ability to encounter, detect, and capture prey ultimately depends on habitat and spatial features (Kunkel and Pletscher 2001). General avoidance of dense conifer stands and north-facing stunted spruce stands by wolves in the BP is probably partially related to ease of movement within territory boundaries. Use of more open forest (i.e., low canopy cover) with low topographic complexity by wolves has been linked to reductions in energy expenditure associated with travel (Paquet 1993; Alexander et al. 2005). Cover is nevertheless important to wolves for providing denning and rendezvous sites, as well as protection and concealment (Mech 1970; Corsi et al. 1999; Theuerkauf et al. 2003; Swan 2005). Wolves in

the BP all den primarily in forested areas (Appendix E, Table E2), and some rendezvous sites have been found in open riparian meadows adjacent to these conifer stands. Selection for both low and high-elevation shrub communities, as well as *Elymus*-dominated burns, increases the likelihood of encountering ungulate prey, particularly moose and elk that are the primary components of wolf diets in the BP (Chapter 5). The use of burned areas by wolves also has been documented in Glacier National Park (Arjo and Pletscher 2004).

In the central Canadian Arctic, home-range selection by wolves was influenced by the availability of eskers, possibly indicating the importance of denning habitat as a potential limiting factor for tundra wolves (McLoughlin et al. 2004). With respect to habitat selection within home ranges, however, wolf movements were not related to specific vegetation communities, but likely to the migratory nature of caribou, the primary prey of wolves in this region. That study highlighted the importance of identifying key landscape features to manage potential conflicts between wolf conservation and future industrial development.

Patterns of selection and avoidance amongst individual packs in the BP were more difficult to assess, but some inter-pack differences still emerged. For example, the Dopp/Keily pack appeared to be more alpine specialists, selecting alpine shrub and open alpine communities across seasons. In contrast, the neighbouring Nevis pack consistently selected lower-elevation shrub communities across seasons. These differences are associated with terrain features within their respective territories. The Dopp/Keily pack's territory encompassed rugged high-elevation terrain associated with the headwater systems of the Besa River and Keily Creek, but many of the hanging basins and high-elevation meadows support high densities of moose and increasing numbers of elk. The range of the

Nevis pack includes rolling terrain more typical of foothills habitat with the wide open Nevis Creek valley running down the middle of their territory. The heavy year-round use of low-elevation riparian areas by both the Pocketknife and Lower Besa packs can be explained by the prevalence of this habitat within their respective ranges at the eastern end of the study area, which is dominated by boreal flats and muskeg. Moose are prevalent on the flats, and elk are available along the mountain range that separates the 2 territories. In Glacier National Park, amongst 6 cover types, pack differences were only observed in the summer when one pack used more open habitat, and the other used more burned areas (Arjo and Pletscher 2004). It was concluded in that study that the use of open habitats was influenced by selection for den and rendezvous sites.

The sign of selection coefficients indicates selection (positive) or avoidance (negative) of particular habitat classes or landscape features (as adjusted by all of the other parameters in the model), and can provide an indication of the importance of variables relative to each other. In addition to my results from resource selection functions, I also presented data on the relative use of habitat classes and landscape features. Data on use can provide more information on the value of habitats. For example, I found consistent selection for open alpine (except during denning), shrub, and alpine shrub habitat classes nearly year round. These habitats together represented approximately 11 % of the available landscape in the BP, and 17 – 35 % of wolf locations were in these areas. Burned habitat types were also selected seasonally by wolves and similar to the shrub class, accounted for approximately 10 % of the BP landscape, but wolves were located in these areas only half as often (7 – 19 %) as they were in the alpine areas. A quarter of the BP landscape was classified as having a complex structure (high fragmentation), but wolves spent nearly half

their time in these areas year round, affording ease of movement and additional hunting opportunities as ungulates use these areas for bedding and security cover for young (Alexander et al. 2005). Over a quarter (28 %) of the BP landscape is covered by conifer-type habitats (pine, spruce, stunted spruce) that wolves tended to avoid, but use was nevertheless high (18 - 24 %) and could be underestimated because of collar performance in these habitat classes (Hebblewhite et al. 2007). I recommend presenting both coefficients from resource selection function analyses and data on relative use to indicate both the direction and magnitude of habitat interactions. Together, this information provides a better understanding of animal distributions on the landscape.

Resource selection models based on habitat class consistently outperformed models based on relative vegetation quality for ungulate prey and models based on NDVI. Both moose and elk are important prey to wolves in the BP. Prey-based models were ranked highest for the Richards pack during the denning and fall seasons, and indicated strong selection for habitat classes that were ranked as relatively high quality for moose. This result is consistent with stable isotope data (Chapter 5) showing that the Richards pack consumed primarily moose during summer (including denning, 54%) and fall (72%) in 2002. It is unclear why more patterns such as this did not emerge. Given relatively high densities of ungulates in the BP, it may be that wolves are using opportunistic hunting routes that maximize encounter rates amongst a diverse range of prey items, rather than focusing on a single species. In addition, the relative selection values for the 4 ungulate species I used in my models may be too specific to track the distribution of a generalist predator in a diverse multi-prey ecosystem.

I had anticipated that NDVI would provide an index of vegetation productivity and quality that would be directly related to the distribution of prey species and subsequently the distribution of wolves in the BP. NDVI is highly correlated with greenness (Tucker and Sellers 1986; Ruimy et al. 1994; Oindo 2002), and greenness has been shown to be correlated with ungulate density (Carroll et al. 2001b). I was able to assess NDVI as a variable only during denning and late summer. In studies of grizzly bears, it has been suggested that greenness and NDVI may be limited in some management applications because high values can be obtained for different habitat types that are functionally diverse (Apps et al. 2004), and may vary by season. Therefore, for wolves, NDVI may be more appropriate at coarser grains of analyses that relate broad patterns of ungulate abundance and distribution to landscape occupancy by wolves, rather than to analyses of use and selection at smaller spatial scales, such as those considered here.

Another vegetation metric that has been used in studies of wolf distribution (e.g., Alexander et al. 2005; Swan 2005) is Tasselled Cap wetness, which is strongly correlated with vegetation structure and soil moisture (Cohen et al. 1995; Todd et al. 1998; Hansen et al. 2001). Wetness may be appropriate at the scales considered here because it may relate more directly to local movement patterns. Selection for wetness in the central Rocky Mountains of Alberta may indicate preference for structurally complex vegetation, potentially increasing the encounter rate with prey species that select more complex vegetation types for bedding, browse, or concealment of young (Alexander et al. 2005). My measure of habitat complexity was fragmentation. High fragmentation areas were consistently selected and used by wolves in the BP. Relative to hierarchical habitat selection, NDVI or greenness may define suitable habitats for wolves at the landscape scale

based on their potential relationship to ungulate densities, but indices such as wetness and fragmentation may provide more detailed information on local movement patterns and habitat selection at finer grains that relate to efficiency and hunting success.

Within home ranges in the BP, wolves used lower elevations during the winter months, and 80% of all locations were on slopes <20°, with the mean <15° across seasons. Selections of different aspects were complex, but overall, north and south aspects were selected seasonally. Wolves commonly travel in areas with ≤15° slope and use SW aspects for winter travel (Singleton 1995; Kunkel 1997). Winter movements of wolves in the central Rocky Mountains follow a downward migration to lower elevations where snow depths are shallower (Paquet et al. 1996). Wolves generally avoid areas of deep snow because of high foot loading, as well as areas with steep slopes where prey vulnerability is low (Paquet et al. 1996). In general, large ungulate prey tend to congregate at lower elevations during the winter (Koehler and Hornocker 1991). In the central Rocky Mountains of Alberta, elk and deer concentrate in vegetated valley bottoms as opposed to steeper, more rugged slopes and ridges (Alexander et al. 2004). Differential use of slope and aspect by predators also may be related to prey availability (Alexander et al. 1996; Arjo and Pletscher 2004). Wolves in northern Italy responded primarily to prey density, but avoided high elevations, steep slopes, and NNE aspects during winter travels (Ciucci et al. 2003).

Selection and avoidance of specific terrain features may enable niche partitioning among sympatric predators (Alexander et al. 2005). In areas where cougars (*Puma concolor*) are abundant in the southern Rocky Mountains, avoidance of rugged terrain by wolves may be a key component in niche partitioning between wolves and cougars (Paquet

et al. 1996; Carroll et al. 2001a). Partitioning of this type may reduce interspecific competition (Alexander et al. 2005). Similarly, coyotes and wolves that use similar habitat types chose different topographic characteristics at finer spatial scales (Arjo and Pletscher 2004). Wolves in the BP selected similar habitat classes to those of grizzly bears (particularly shrub communities), but they typically were found at lower elevations than grizzly bears during different seasons of the year, and they exhibited different elevational movement patterns (Chapter 4). Wolves and grizzly bears are the top predators in the BP, and ungulates can account for a significant proportion of both species' seasonal diets (Chapter 5). Spatial segregation has also been observed at broad spatial scales. In southwestern Alaska where black bears and brown bears segregate spatially from wolves when killing moose calves (Garneau et al. 2007), researchers maintained the possibility that these predators also partitioned space within finer-scale habitat classes that they were unable to identify. Bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) coexisting in California did not show spatial segregation at the landscape scale, but they did display differential habitat use (and avoidance) at the home-range scale (Neale and Sacks 2001). The role of niche partitioning in the BP merits further investigation.

I was unable to correct for habitat and terrain-induced GPS-collar bias for wolf locations because I did not have local models predicting GPS fix acquisition as a function of terrain and land-cover characteristics (see Frair et al. 2004). In general, RSF coefficients need to be interpreted with caution, but the deployment of multiple collars in each pack reduced data loss. Indeed there were many occasions when a fix was acquired by one collar and not another. A recent study in the Canadian Rocky Mountains found significant habitat and terrain-induced bias associated with conifer and aspen stands and narrow mountain

valleys, and differences in fix acquisition among collar brands, but also indicated that >50 % of data lost from collars deployed on wolves was due to wolf behaviour that cannot be corrected (Hebblewhite et al. 2007). Conifer and aspen stands cover 1/3 of the BP, and valleys are generally wider than 500 m, so potential collar bias in my system may be less than those found in other mountainous terrain. Furthermore, wolves are unlikely to spend a considerable amount of time in dense conifer stands that are less productive for ungulates than other available habitats.

My research provides information on habitat use and selection by wolves that will be applicable to the long-term management of this population. My findings corroborate the biological linkages between wolves and their habitat related to ease of movements, prey distribution and rates of encounter, and niche differentiation between sympatric carnivores.

Chapter 4: Temporal Variation in Habitat Selection by Grizzly Bears in Northern British Columbia.

Introduction

The conservation of grizzly bears (*Ursus arctos*) is a high-profile wildlife management issue in North America. The issue encompasses concerns about land-use practices, as well as the impacts of hunting and other human-caused mortality (Mowat et al. 2005). Industrial resource-extraction activities threaten the persistence of grizzly bears by fragmenting habitats and increasing access by humans to previously remote landscapes (Banci et al. 1994; Clark et al. 1996; McLellan 1998; Nielsen et al. 2004a). In the Central Rocky Mountains Ecosystem of Canada, unprecedented growth of the human population and resource extraction has co-occurred (Schneider et al. 2003), amplifying human-caused mortality, which is the primary source of death for grizzly bears (Benn and Herrero 2002, Nielsen et al. 2004b). In the northern Rocky Mountains of British Columbia, expanses of wilderness still remain relatively free of human disturbance and with minimal opportunities for access. The impending expansion of the oil and gas and mining industries into this region, however, poses significant challenges for the future management and conservation of grizzly bears across this wilderness landscape. Identifying habitats that are important to grizzly bears in both a spatial and temporal context is an important first step in developing a management and conservation strategy that could incorporate resource-extraction values and wildlife needs.

Optimal habitats for grizzly bears generally are considered road-less areas with a mosaic of early seral-staged forests and natural openings in proximity to secure forest stands that provide day beds and hiding cover (Herrero 1972; Blanchard 1983; Hamer and Herrero

1987). Loss of these types of habitats has the potential to cause population declines in bears (McLellan and Hovey 2001). Habitat selection by grizzly bears varies seasonally (e.g., McClellan and Hovey 1995, 2001). In mountainous landscapes, the importance of avalanche chutes and unforested alpine habitats has been documented (Waller and Mace 1997; McClellan and Hovey 2001). Grizzly bears in landscapes of higher forest productivity with mature-to-old stands of mixed-species composition also use a relatively high proportion of open habitats (Apps et al. 2004). The forested habitats may provide opportunities for thermal regulation and security (Blanchard 1983; McClellan 1990). At finer scales, a positive association with higher open-habitat composition has been related to the potential influence of herbaceous forage value on daily movements (Apps et al. 2004). Areas burned by fire often are highly preferred because of high berry production (Hamer and Herrero 1987; McClellan and Hovey 2001).

Habitat models for grizzly bears have been generated for several areas, including Idaho and Montana (Boyce and Waller 2000, 2003; Mace et al. 1996, 1999), British Columbia (McLellan and Hovey 2001; Apps et al. 2004; Ciarniello et al. 2007), Alberta (Franklin et al. 2001; Nielsen et al. 2004a,b,c), and the Northwest Territories and Nunavut (McLoughlin et al. 1999) using animal radio-telemetry locations, remote-sensing data for vegetation classifications and habitat surrogates such as greenness, and habitat selection modeling. This approach relies on geographic information systems (GIS) and remote-sensing data that are available across large spatial extents. When related to animal locations, these data are useful in generating inferences on patterns of habitat selection and relative habitat quality that are readily applicable to conservation and management (Nielsen et al. 2003).

In addition to habitat modeling techniques based on GIS and remote sensing, resource selection functions (RSFs) (Manly et al. 1993) provide information about essential resources required to manage and conserve rare, threatened, and endangered species in increasingly complex socio-environmental landscapes (Nielsen et al. 2002). Although RSF models do not provide a ready comparison of fitness among individuals (Garshelis 2000) and their probabilistic properties for predicting occurrence have been challenged (Keating and Cherry 2004), they do provide an objective and explanatory framework to assess habitat selection and relative habitat quality at multiple scales and across individuals and populations (Nielsen et al. 2002). RSF models for grizzly bears have been developed for the Rocky Mountain region of the United States (Mace et al. 1996, 1999; Boyce and Waller 2000) and the Northeast Slopes region of the Canadian Rocky Mountains of western Alberta (Nielsen et al. 2002). These models were developed for regions that have some level of human development with the goals of understanding current grizzly bear population dynamics in response to human activities, predicting the capacity of the landscape to support grizzly bears, or determining the potential to reintroduce grizzly bears into previously occupied landscapes. In contrast, northern British Columbia (BC) provides an opportunity to examine and model habitat use and selection by grizzly bears in a relatively undisturbed setting, providing valuable baseline data on grizzly bear ecology that will enable management decisions in advance of development activities.

I describe robust RSF models for female grizzly bears in the northern Rocky Mountains of BC. I focus on 3rd order selection (i.e., within the home range, Johnson 1980) across and within individuals over 3 seasons and multiple years using variables believed to be important to grizzly bears. I compare 3 types of models to understand whether habitat

class (based on remote-sensing data of vegetation classifications), habitat productivity or quality (based on vegetation indices using a Normalized Difference Vegetation Index [NDVI]), or the selection value for prey (based on relative resource selection values for the major ungulate prey species) most influences the spatio-temporal dynamics of grizzly bears in the Besa-Prophet study area of northern BC. Additonally, I describe resource selection patterns in the context of relative habitat use by grizzly bears across the landscape. I present data from individual grizzly bears because I was interested in exploring details of grizzly bear ecology, and the degree of variability across the system. This analysis was conducted concurrently with analyses of resource selection by wolves (Chapter 3). By taking a comprehensive look at home-range sizes constrained by resource availability (Chapter 2), resource selection patterns within these home ranges, the degree of variability amongst these 2 top predators, and taken in the context of seasonal prey consumption (Chapter 5), we begin to see the level of complexity inherent in managing for resource development.

Study Area

The Muskwa-Kechika Management Area (MKMA) in northern BC covers approximately 6.4 million ha. Within the MKMA, my research was focused in the Besa-Prophet study area (BP). The BP included the 204,245-ha Besa-Prophet pre-tenure planning area (a zone managed for resource exploration and development), the 80,771-ha Redfern-Keily Provincial Park, and portions of surrounding areas for a total of 740,887 ha between 57°11' and 57°15' N latitude, and 121°51' and 124°31' W longitude. Three biogeoclimatic zones are found within the region (Meidinger and Pojar 1991). The boreal white and black spruce (BWBS) zone covers the 3% of the BP characterized by white and black spruce (*Picea glauca* and *P. mariana*) at low elevations. The spruce-willow-birch (SWB) zone of

sub-alpine spruce, willow (*Salix sp.*), and birch (*Betula glandulosa*) covers 81% of the BP, and alpine tundra (AT) encompasses 18% of the BP at elevations >1600 m. Valleys in the BP at ~800-1300 m are lined with white spruce, some lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*) on dry sites, and black spruce, willow-birch communities on poorly drained sites. South aspects often have burned grassland vegetation and deciduous trees. The SWB is typically the sub-alpine zone above the BWBS in northern BC. It is characterized by an abundance of willow and scrub birch, as well as some balsam fir (*Abies lasiocarpa*) and white spruce often in krummholz form, and various grasses, sedges and fescues (*Festuca* spp.). The alpine zone is usually treeless, unless trees are in stunted or krummholz form. It is dominated by a dwarf scrub of prostrate woody plants and herbs such as *Dryas* spp. and *Cassiope* spp., bryophytes, and lichens; or rock and permanent snowfields (Demarchi 1996). The topography of the BP is an interlaced network of north-south ridges, and east-west valleys with a prominence of south-facing slopes. The BP supports one of the most diverse predator-prey ecosystems in North America. Ungulates include moose (*Alces alces*), elk (*Cervus elaphus*), caribou (*Rangifer tarandus caribou*), Stone's sheep (*Ovis dalli stonei)*, and a few mountain goats (*Oreamnos americanus*) and deer (*Odocoileus* spp.). Predators capable of preying on these ungulates include wolves (*Canis lupus*), grizzly bears, black bears (*U. americanus*), cougars (*Felis concolor*), coyotes (*Canis latrans*), and wolverines (*Gulo gulo*), although it is believed that only wolves and grizzly bears are of sufficient numbers to be capable of limiting or regulating the ungulate communities.

Methods

Bear Capture and Locational Data

Twenty-seven grizzly bears were captured and fitted with GPS collars (Simplex, Televilt, Lindesberg, Sweden) between May and June 2001-2003. Male bears easily shed their collars, and therefore, the few data from males were not included in analyses. Collars were programmed to acquire locations every 6 hr (0100, 0700, 1300, 1900) for 2-3 years. Some collars were replaced during the course of the study, some collars failed, and some bears were captured later in the study resulting in a range of 1-4 years of data from individual bears. I secured GPS data via remote download or collar retrieval. I present data acquired from 13 female grizzly bears for which complete years of GPS locations were available. Grizzly bears in the central interior of BC show bimodal circadian patterns of activity and are least active after mid-night and during mid-afternoon hours (1000 – 1600 hr) (Heard et al. 2008). The interaction of canopy cover and sub-optimal collar orientation associated with resting resulted in collar bias and lost fixes. The circadian pattern declines during the fall. Consequently, I examined collar performance in relation to possible behavioural influences using a two-way ANOVA. In this model I examined fix rates as a function of season, time-of-day (6-hr intervals), and their interaction (season*time-of-day). If there was a behavioural component to collar bias, I expected fix rates at 0100 and 1300 to be significantly lower than at other times, except during the fall when bears are expected to be most active during hyperphagia. I used Tukey's HSD test to identify pairwise differences following a significant ANOVA.

Study Design

Telemetry locations were used to estimate resource use, and then compared to randomly sampled locations using logistic regression to quantify selection (Manly et al. 1993; Boyce and MacDonald 1999). I defined availability as all areas within 95 % annual minimum convex polygon (MCP) home ranges, given my observation that 5 % of locations at the periphery of a grizzly bear's home range that were related to extra-territorial movements arbitrarily increased home ranges by 30 to 100 %. I defined MCPs using the animal movement extension (Hooge et al. 1998) in Arcview 3.2™ (Environmental Systems Research Institute, Redlands, Calif., U.S.). To characterize availability, 5 available points per use point (e.g. Ciarniello et al. 2007) were randomly generated within each annual and seasonal MCP for each bear and year using the random point generator extension (Jenness 2003) in Arcview 3.2. I identified 3 seasons for bears based on plant phenology: spring (den emergence - 15 June), summer (16 June - 15 August), and fall (16 August - denning). For a season to be included in analyses, $\geq$50 use points for that season were needed to satisfy issues of sample size and model separability. Coefficients from logistic regression analyses were used to estimate RSFs by year and season for all bears and each individual.

GIS and Remote Sensing Data

Vegetative and topographical variables in resource selection model sets for bears were 25-m resolution raster GIS data. A digital elevation model (DEM) was obtained from the 1:20,000 British Columbia Terrain and Resource Inventory Management program (British Columbia Ministry of Crown Lands 1996) to create slope and aspect layers. Aspect was categorized into north (315 - 45°), east (45 - 135°), south (135 - 225°), and west (225 - 315°) directions. Pixels with slope $\leq$1° were assigned no aspect (NAS). For all selection

models, elevation (km) and slope (°) were entered as quadratic terms. Vegetation classes were identified using an August 2001 Landsat Enhanced Thematic Mapper 7 image and classified based on 227 field training sites with an overall classification accuracy of 77% (Lay 2005). I combined the initial 15 vegetation classes into 10 major habitat classes (Table 4.1). Classes were lumped according to similarity of vegetation and elevation, and possible prey associations (e.g., moose and riparian spruce; elk and deciduous burns; caribou and open alpine; Stone's sheep and *Elymus* burns). An index of vegetation fragmentation was created from the initial vegetation classes that were grouped according to open, closed, or unique cover types (Gustine 2006b) and was used as a measure of habitat diversity. Each pixel was classified relative to the proportions of different cover types in a moving 7 by 7 pixel-sized window, and then categorized as low, medium, or high fragmentation, as in Gustine (2005). Any categorical class for which there was no use by grizzly bears was omitted from selection models (Menard 2002). There were no cases for which there were zero availability.

Seasonal differences in multi-temporal Normalized Difference Vegetation Index (NDVI) values have been used to explain movements of wildlife species in numerous studies (Lay 2005). The Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) onboard Landsat satellites capture multi-spectral data at 30-m resolution. I used NDVI images generated by Lay (2005) from 14 TM and ETM+ images during the 2002 growing season in the BP. Because NDVI is correlated with plant biomass (Tucker and Sellers 1986; Ruimy et al. 1994) and the change in NDVI is correlated with vegetation quality (Oindo 2002), I substituted NDVI and change in NDVI for habitat classes in

Table 4.1. Habitat classes used in analyzing habitat selection by grizzly bears in the Besa-Prophet study area of northern British Columbia, 2001-2004, along with availability across the study area.

Habitat classes	% of Study Area	Description
Conifer	22.3	Dense mid-elevation pine (*Pinus contorta*) and white and hybrid spruce (*Picea glauca, P. mariana x glauca*)-dominated forest stands.
Stunted Spruce	5.6	Open spruce areas typical of north-facing slopes.
Shrub	5.7	Willow (*Salix* spp.) and birch (*Betula glandulosa*) shrub communities ≤1600 m.
Alpine Shrub	5.7	Willow and birch shrub communities >1600 m.
Non-Vegetated	23.7	Rock (boulder, talus), rock-lichen associations, water, snow.
Riparian Spruce	17.7	Low elevation (<1600 m) wetland spruce (*P. glauca* or *P. mariana* in poorly drained sites) along streams; includes gravel bars and sedge (*Carex* spp.) meadows.
Open Alpine	5.5	Dry alpine tundra habitat >1600 m characterized by *Dryas* spp.; wet alpine tundra habitat >1600 m dominated by *Cassiope* spp. and sedge (*Carex* spp.) meadows.
Deciduous Burns	7.1	Older burns; characterized by deciduous shrubs and regenerating young aspen/poplar (*Populus tremuloides* and *P. balsamifera*) stands.
Elymus Burns	3.2	Younger burns; meadows dominated by *Elymus innovatus*.
Sub-alpine Spruce	3.5	Open spruce; transition zone between dense mid-elevation spruce stands and open alpine areas.

competing models to determine whether habitat class per se or vegetation biomass or quality was more important in driving selection patterns of grizzly bears.

Concurrent with this study, GPS data were collected on the distribution and locations of moose (Gillingham and Parker 2008a), Stone's sheep (Walker et al. 2007), and caribou (Gustine 2005; Gustine et al. 2006b) in the BP to form RSFs that identified habitat selection by season. These logistic regression models incorporated GPS data, habitat class, elevation (km), slope, aspect, the index of fragmentation, curvature (an index of concavity or convexity in Stone's sheep models only), vegetation biomass and quality, and an index of predation risk from wolves and grizzly bears (details in Gustine 2005; Gustine et al. 2006a,b; Walker 2005; Walker et al. 2007). Habitat values for elk in the BP were modelled previously in a conservation area design for the area (Heinemeyer et al. 2004a, b). I used these prey selection models to estimate potential prey benefit of these 4 ungulate species to grizzly bears. The final models used to generate these prey benefit surfaces are presented in Appendix C; Table C1. I scaled values between 0 and 1 to standardize prey selection surfaces (Manly et al. 1993). I then incorporated combinations of these standardized layers into models competing with those generated from vegetative and topographic features to determine the extent to which high selection values for potential prey may contribute to the habitat selection patterns of grizzly bears.

Modelling Procedures

Given the lack of information on habitat-use patterns by grizzly bears in the study area, I acknowledge that model development to define selection was an exploratory process using different combinations of the afore-mentioned variables to obtain the best assessment of habitat selection (Burnham and Anderson 2002). I constructed individual models as well

as global models for which I pooled GPS locations across years and individuals. Categorical variables were coded with deviation contrasts (Menard 2002). I ran 32 models during spring and fall, and 44 during summer for each year per individual, and across individuals, seasons, and years (Appendix C; Table C2).

To avoid inflating selection coefficients and associated standard errors (Menard 2002), I assessed collinearity among variables by season. Given the relatively high number of parameters in my exploratory model sets and the number of models generated, I used a tolerance score of <0.3 to assess potential collinearity (Sokal and Rohlf 2000). I ran separate models for correlated variables. For example, vegetation biomass, vegetation quality, and an interaction term (biomass x quality) were entered as separate variables in competing models given the high degree of collinearity (tolerance <0.3) among variables.

I used Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) to select the best model(s) from a suite of model combinations that were compared by season for all grizzly bears. Akaike's Information Criterion corrected for small sample sizes (AIC_c, $n/K < 40$) was used to rank the model sets for individual grizzly bears (Burnham and Anderson 2002). At large sample sizes (n), AIC_c equals AIC (Burnham and Anderson 2002). The lowest AIC_c in a model set indicates the model that likely explains the greatest amount of variation in the data with the fewest parameters possible (parsimony). Differences in AIC_c (Δ_i) provide an estimate of the distance that a candidate model is from the true model (Burnham and Anderson 2002). Akaike weights (w_i) give an estimate of the relative probability that the top model is the best amongst the suite of candidate models. A single model was selected as the likely top model if $w_i \geq 0.90$. If the top model had an associated $w_i < 0.90$, I averaged the selection coefficients (β_i) from the suite of top

candidate models for which $\sum w_i \geq 0.95$ (i.e., one can state with 95% confidence that the top model is in the set; Burnham and Anderson 2002). I used the *k*-fold cross-validation procedure averaged across 5 random subsets and a Spearman's rank correlation (r_s) (Boyce et al. 2002; Nielsen et al. 2002) to determine the predictive ability of each top model. Values of $r_s > 0.70$ indicated good model performance (Boyce et al. 2002).

Results

I retrieved 12,397 GPS locations from 13 female grizzly bears between June 2001 and October 2004. Fix rates averaged 67% ± 13% across individuals ($\overline{X}$ ± SE; $n = 13$; range = 41 - 82%). Annual 95% MCPs ranged from 82 to 662 km^2 (see Chapter 2). Fix rates were not a function of season ($F_{(2,180)} = 0.69$, $P = 0.50$). Time of day effected fix rates ($F_{(3,180)} = 12.84$, $P < 0.001$), but there was no interaction between season and time-of-day ($F_{(6,180)} = 1.11$, $P = 0.36$). Across seasons, mean fix rates at 0100 were significantly lower than all other times. Differences between mean fix rates at all other times were not significant.

Pooled Habitat Use and Selection Across Grizzly Bears

Habitat Use

Across individuals, female grizzly bears commonly used higher elevations during spring ($\overline{X}$ = 1597 m, range = 1400 - 1750 m) and the lowest elevations during fall ($\overline{X}$ = 1432 m, range 1100 - 1500 m). They used the broadest range of elevations during summer ($\overline{X}$ = 1550, range 1100 - 1750 m). This pattern was generally consistent among years, with the exception of 2002 when bears could be found at higher elevations during the summer (Fig. 4.1).

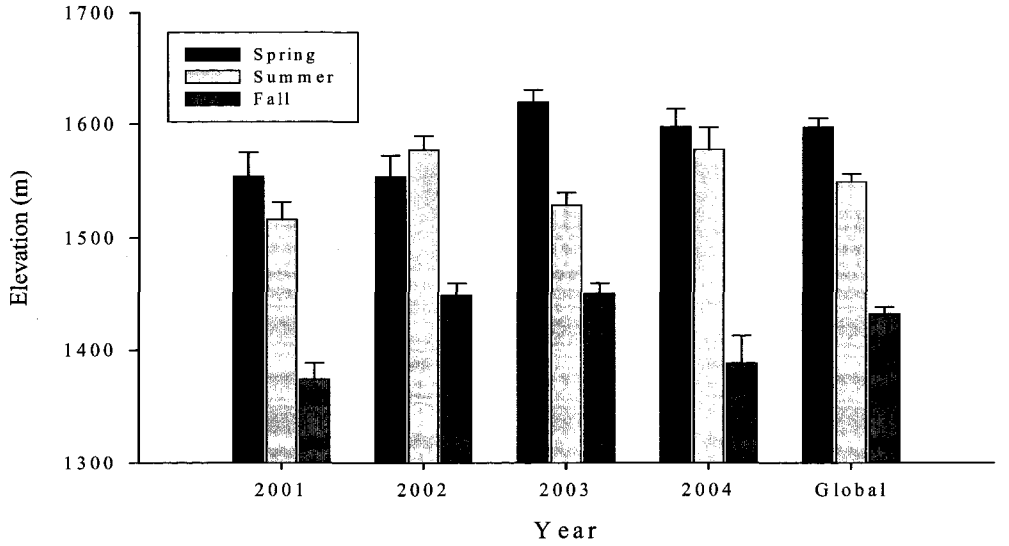

Figure 4.1. Pooled elevations (mean ± SE) used during spring (den emergence – 15 June), summer (16 June – 15 August), and fall (16 August – denning) by 13 female grizzly bears within and across (global) years in the Besa-Prophet study area of northern British Columbia, 2001-2004.

Use of the categorical variables habitat class, fragmentation, and aspect by grizzly bears varied across seasons (Tables 4.2, 4.3). During the spring (n = 3013), grizzly bears spent almost half their time (48.4 %) in alpine environments (alpine shrub, non-vegetated, open alpine). Use of alpine shrub (26.8 %) communities peaked in summer (n = 4774) and highest use of conifer (20.5 %) and shrub (13.1%) classes occurred during fall (n = 4610). The use of other habitat classes by grizzly bears was relatively consistent across seasons. For example, the burn habitat classes comprised approximately 10 % of the locations across seasons. Approximately half the locations (45.2 - 51.9 %) were in the most complex habitats as measured by fragmentation, and about a third (31.1 - 35.5 %) were in moderately complex habitats. Grizzly bears tended to use east (29.3 %) and south aspects (39.1 %) most during the spring, and their use of north aspects increased during summer (25.0 %) (Table 4.3). In fall, highest use was again on south aspects (34.1 %). Use of west aspects and flat terrain was consistently low across seasons.

Seasonal Selection

The best global models of selection across years consistently contained the most parameters, or were averaged with models containing the most parameters (Appendix C, Table C3). Model performance as estimated by Spearman's rank correlation (r_s) was high overall, ranging from 0.79 to 0.99. Habitat class, fragmentation, aspect, and elevation were attributes in all of the top seasonal models (with the exception of spring 2002). Vegetation biomass (spring 2001), vegetation quality (summer 2004), and slope (spring 2002; summer 2004) were also important attributes in some seasons.

Specific habitat classes (Fig. 4.2) and landscape (Fig. 4.3) features were consistently selected or avoided by grizzly bears in the BP. Across seasons, grizzly bears avoided

Table 4.2. Summary of % relative use (U) versus availability (A) of habitat classes (as defined in Table 4.1) by female grizzly bears in the Besa-Prophet study area of northern British Columbia. Seasonal GPS locations were pooled across individuals and years (global), across individuals within year, and by individual across years (2001-2004).

Bear	Season	Conifer		Stunted Spruce		Shrub		Alpine Shrub		Non-Veg.		Riparian Spruce		Open Alpine		Decid. Burns		*Elymus* Burns		Sup-alpine Spruce	
		U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A
Global	Spring	13	21	6	6	3	5	15	12	19	23	4	6	15	11	10	6	10	3	6	6
	Summer	13	20	5	6	7	6	27	12	6	26	7	6	7	11	12	6	6	3	10	5
	Fall	21	22	8	6	13	5	10	12	6	24	11	6	3	11	11	6	10	3	7	5
2001	Spring	17	28	4	5	8	6	8	7	11	18	4	10	23	9	9	9	12	4	5	5
	Summer	17	24	3	6	9	6	18	11	4	19	5	8	5	11	18	7	7	4	15	5
	Fall	17	25	12	6	14	6	8	11	4	15	15	8	2	11	13	8	7	4	8	6
2002	Spring	16	26	4	6	3	7	14	11	14	16	3	7	9	10	17	8	13	3	6	6
	Summer	11	19	4	4	9	6	30	12	6	31	6	5	7	10	12	5	6	3	10	5
	Fall	19	19	8	4	11	6	12	13	8	29	10	6	4	10	10	5	11	2	6	5
2003	Spring	13	19	4	5	3	5	17	14	21	29	3	5	17	10	9	4	8	3	5	6
	Summer	15	20	5	6	6	6	26	12	6	25	8	6	6	11	12	5	6	3	10	5
	Fall	24	23	7	7	14	5	10	12	5	23	8	6	3	11	11	6	9	3	9	5
2004	Spring	11	21	11	8	2	5	13	11	21	20	5	6	12	12	9	7	10	4	6	6
	Summer	10	18	6	7	5	4	32	14	7	23	9	6	13	12	9	6	5	4	6	5
	Fall	12	20	7	9	14	4	8	10	6	22	20	6	4	12	10	6	15	5	4	5

Table 4.2 Continued

Bear	Season	Conifer		Stunted Spruce		Shrub		Alpine Shrub		Non-Veg.		Riparian Spruce		Open Alpine		Decid. Burns		*Elymus* Burns		Sup-alpine Spruce	
		U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A
G01	Spring	8	22	7	9	1	6	28	15	17	8	0	5	17	15	7	8	7	5	7	7
	Summer	14	23	8	8	5	6	25	16	8	7	6	6	11	14	9	9	8	5	8	7
	Fall	14	23	15	9	7	6	9	16	4	7	7	7	3	14	17	8	17	4	7	8
G05	Spring	11	31	4	6	2	9	8	6	8	8	0	12	23	8	20	10	19	5	5	5
	Summer	9	29	2	7	20	10	12	6	1	8	8	11	4	7	21	12	8	6	14	4
	Fall	16	30	10	6	19	9	1	6	4	6	19	12	2	8	18	11	8	5	4	4
G08	Spring	21	13	4	2	7	3	16	9	16	53	10	4	6	7	6	2	5	1	9	5
	Summer	18	14	1	2	11	3	22	8	7	56	8	3	2	8	15	2	2	1	15	4
	Fall	22	12	2	1	17	3	16	7	4	59	14	3	2	7	4	2	8	1	11	4
G15	Spring	21	32	17	15	2	5	2	5	11	8	7	9	14	10	9	8	12	5	5	4
	Summer	19	30	13	17	4	2	2	4	5	12	17	8	6	9	15	7	8	6	12	4
	Fall	18	33	14	17	15	3	2	4	3	10	24	7	1	9	5	7	7	6	12	3
G18	Spring	17	25	7	8	5	7	17	16	9	6	2	5	15	14	8	8	11	4	8	7
	Summer	15	26	5	8	5	7	30	15	2	8	5	6	10	13	9	7	5	3	14	7
	Fall	25	28	11	7	17	8	8	14	3	6	10	5	2	15	13	7	3	3	8	6

Table 4.2 Continued

Bear	Season	Conifer		Stunted Spruce		Shrub		Alpine Shrub		Non-Veg.		Riparian Spruce		Open Alpine		Decid. Burns		*Elymus* Burns		Sup-alpine Spruce	
		U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A
G20	Spring	31	28	14	8	5	10	12	16	5	6	6	7	5	10	11	6	4	2	6	6
	Summer	24	28	12	9	9	11	10	9	2	7	13	7	5	12	6	7	6	3	12	7
	Fall	25	29	10	9	15	10	8	10	4	7	12	7	2	11	10	7	5	4	9	6
G21	Spring	8	7	0	0	2	3	10	9	66	62	1	2	8	8	1	4	1	2	5	4
	Summer	4	6	1	0	5	4	30	9	15	62	2	3	6	7	19	3	9	1	10	5
	Fall	6	7	0	0	6	3	26	10	28	61	4	2	3	7	8	5	7	1	12	5
G22	Spring	14	22	4	5	1	3	7	16	29	30	6	7	32	8	2	3	2	2	2	5
	Summer	21	21	3	5	5	3	22	14	5	31	8	6	4	10	4	3	7	2	20	6
	Fall	30	22	7	5	7	3	13	15	3	29	6	5	6	9	5	4	14	2	9	7
G23	Spring	10	7	2	1	9	3	9	17	21	48	1	1	14	10	20	5	4	2	9	5
	Summer	7	10	2	1	7	5	39	13	11	48	3	2	9	9	11	6	5	3	6	3
	Fall	10	12	0	1	23	5	10	12	5	47	10	4	16	9	1	5	16	2	8	3
G24	Spring	11	21	3	5	0	3	36	12	8	29	1	5	25	14	6	4	5	2	5	5
	Summer	6	23	3	5	2	3	57	14	3	28	3	6	13	12	6	2	0	1	7	6
	Fall	33	21	13	5	2	2	7	16	13	28	6	6	7	11	5	4	10	2	4	5

Table 4.2 Continued

Bear	Season	Conifer		Stunted Spruce		Shrub		Alpine Shrub		Non-Veg.		Riparian Spruce		Open Alpine		Decid. Burns		*Elymus* Burns		Sup-alpine Spruce	
		U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A	U	A
G25	Spring	1	13	0	1	3	5	24	20	19	29	1	3	13	15	19	4	16	4	2	6
	Summer	3	14	1	1	8	6	42	20	6	28	2	5	9	14	18	5	9	3	3	4
	Fall	13	14	4	1	17	7	19	22	6	26	8	4	5	13	16	4	7	3	5	5
G26	Spring	5	12	1	2	1	6	8	15	53	39	6	4	12	12	3	3	8	3	3	5
	Summer	4	10	4	3	3	5	46	18	8	37	5	4	12	13	9	3	5	3	3	4
	Fall	19	10	2	2	15	3	16	17	6	42	8	3	5	12	5	2	20	4	4	4
G27	Spring	5	37	16	34	1	3	1	1	10	7	5	8	1	7	19	14	24	5	1	2
	Summer	35	36	9	11	10	9	1	1	1	9	21	10	1	7	16	11	5	5	1	1
	Fall	36	34	4	14	18	8	0	1	0	10	11	10	1	7	18	9	11	4	0	2

[a] Spring = den emergence - 15 June; Summer = 16 June - 15 August; Fall = 16 August - denning.

Table 4.3. Relative use (%) of vegetation diversity (fragmentation) and aspect by female grizzly bears in the Besa-Prophet study area of northern British Columbia. Seasonal GPS locations were pooled across individuals and years (global), across individuals within year, and by individual across years (2001-2004). NAS = No Aspect (<1° slope).

		Fragmentation			Aspect				
Bear	**Season[a]**	**Low**	**Medium**	**High**	**N**	**E**	**S**	**W**	**NAS**
Global	Spring	17	31	52	13	29	39	17	1
	Summer	19	35	45	25	28	29	15	3
	Fall	19	32	49	22	24	34	16	3
2001	Spring	11	28	61	14	28	42	15	1
	Summer	21	33	46	23	31	31	13	2
	Fall	15	30	55	20	21	35	20	4
2002	Spring	25	31	44	12	28	41	18	2
	Summer	20	37	43	25	29	30	15	2
	Fall	22	34	44	19	23	37	17	3
2003	Spring	18	34	49	14	32	38	16	1
	Summer	20	37	43	26	27	27	17	4
	Fall	18	33	49	25	27	31	15	2
2004	Spring	14	29	58	12	27	39	21	1
	Summer	15	30	54	26	29	30	12	3
	Fall	14	27	59	19	24	31	17	8
G01	Spring	11	30	59	6	31	37	26	0
	Summer	17	31	52	29	28	27	13	2
	Fall	14	34	52	13	26	41	17	2
G05	Spring	21	29	50	9	28	52	11	0
	Summer	28	32	40	21	27	29	19	3
	Fall	15	31	54	18	17	26	35	4
G08	Spring	14	26	60	24	24	35	14	3
	Summer	15	32	53	18	26	40	11	5
	Fall	24	28	49	22	25	36	12	5
G15	Spring	11	34	55	17	42	16	25	1
	Summer	17	28	55	28	44	9	15	4
	Fall	8	19	73	32	25	26	10	6
G18	Spring	6	34	60	11	18	47	23	<1
	Summer	19	35	46	35	29	20	13	2
	Fall	15	31	54	19	21	38	20	3

Table 4.3 Continued

		Fragmentation			Aspect				
Bear	**Season[a]**	**Low**	**Medium**	**High**	**N**	**E**	**S**	**W**	**NAS**
G20	Spring	11	36	53	25	33	14	26	2
	Summer	15	35	50	29	26	24	15	6
	Fall	18	30	52	20	22	35	18	5
G21	Spring	38	25	37	21	27	31	20	0
	Summer	17	33	50	14	28	40	18	0
	Fall	25	22	53	17	32	37	13	1
G22	Spring	18	34	48	15	39	29	14	3
	Summer	20	42	38	31	28	21	17	3
	Fall	25	40	35	23	32	31	12	2
G23	Spring	18	50	32	12	30	49	9	0
	Summer	22	44	35	32	20	31	17	1
	Fall	12	38	49	19	8	42	23	7
G24	Spring	20	34	47	14	37	33	16	0
	Summer	26	43	31	32	38	16	13	0
	Fall	23	37	40	42	20	34	4	<1
G25	Spring	17	45	38	6	31	59	5	0
	Summer	20	46	35	20	26	38	15	<1
	Fall	23	36	41	21	20	40	15	4
G26	Spring	34	28	39	8	37	44	10	1
	Summer	23	37	40	15	21	40	17	6
	Fall	19	44	37	23	24	27	23	4
G27	Spring	12	14	75	9	14	45	29	3
	Summer	11	29	59	24	37	21	11	7
	Fall	19	41	40	23	45	20	6	7

[a] Spring = den emergence to 15 June; Summer = 16 June - 15 August; Fall = 16 August - denning.

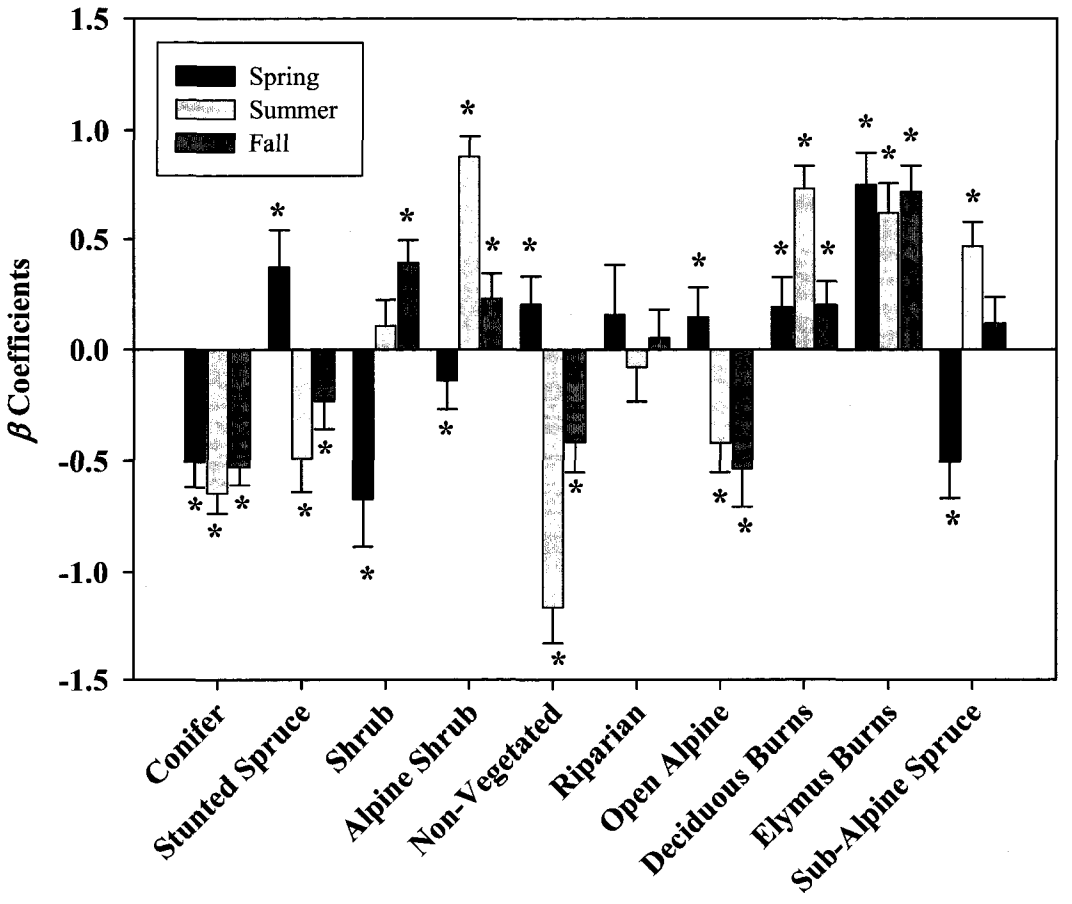

Figure 4.2. Seasonal selection patterns by grizzly bears for habitat classes in the Besa-Prophet study area of northern British Columbia, pooled across years (2001-2004).
* identifies significant coefficients as determined by the 95 % confidence interval that does not encompass 0. Coefficients >0.0 indicate selection, and <0.0 indicate avoidance.

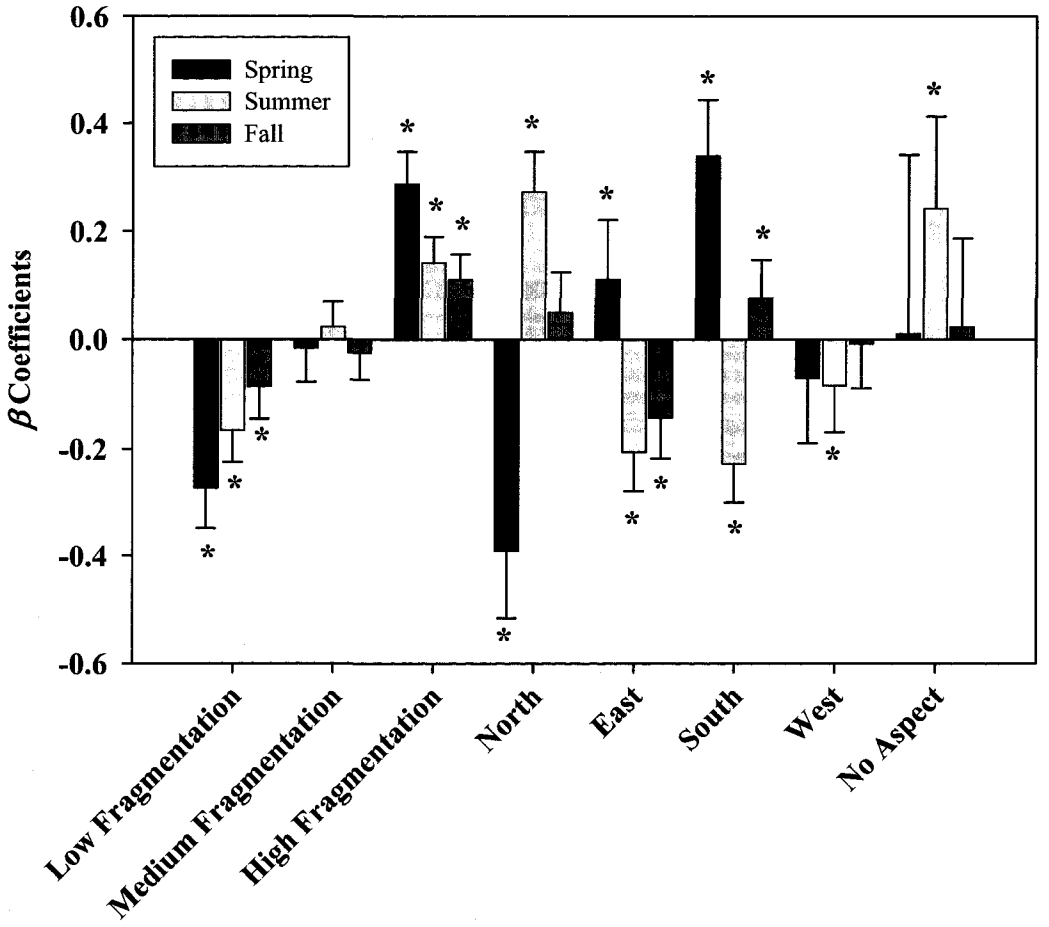

Figure 4.3. Seasonal selection patterns by grizzly bears for landscape features in the Besa-Prophet study area of northern British Columbia, pooled across years (2001-2004).
* identifies significant coefficients as determined by the 95 % confidence interval that does not encompass 0. Coefficients >0.0 indicate selection, and <0.0 indicate avoidance. No Aspect <1° slope.

conifer stands and low-fragmentation areas, and selected burned vegetation types (deciduous burns, *Elymus* burns), and high-fragmentation areas. Grizzly bears were more variable in their selection of other vegetative and landscape features across seasons. Grizzly bears selected stunted spruce, non-vegetated, and open alpine habitat classes, as well as east aspects in the spring, but avoided these features during the summer and fall. Shrub-type habitats were avoided in the spring and usually selected during the summer and fall. Grizzly bears avoided north aspects during the spring but selected for north-facing slopes in the summer, and they selected for south aspects during the spring and fall but tended to avoid these areas in the summer. None of the top global models for grizzly bears included coefficients for habitat selection values for prey, and only 1 individual pooled model (G20) included these coefficients (Appendix C, Table C3).

Habitat Use and Selection Among Individual Bears

Habitat Use

Eleven of the 13 grizzly bears used elevations that averaged >1500 m during spring; and 7 of those individuals' locations averaged >1600 m (Fig. 4.4). Nine grizzly bears remained at mean elevations >1500 m during the summer. Only 2 grizzly bears used mean elevations >1500 m during the fall. One grizzly bear (G21) was an alpine specialist using mean elevations >1600 m year-round, in contrast to another individual (G27) that was a riparian specialist with average elevations <1400 m across seasons.

Individual grizzly bears were highly variable in their use of different habitat classes across seasons (Table 4.2). Changes in use by the majority of individuals (but not all) were reflective of the patterns of use across individuals. In spring, most bears (9 of 13) were in

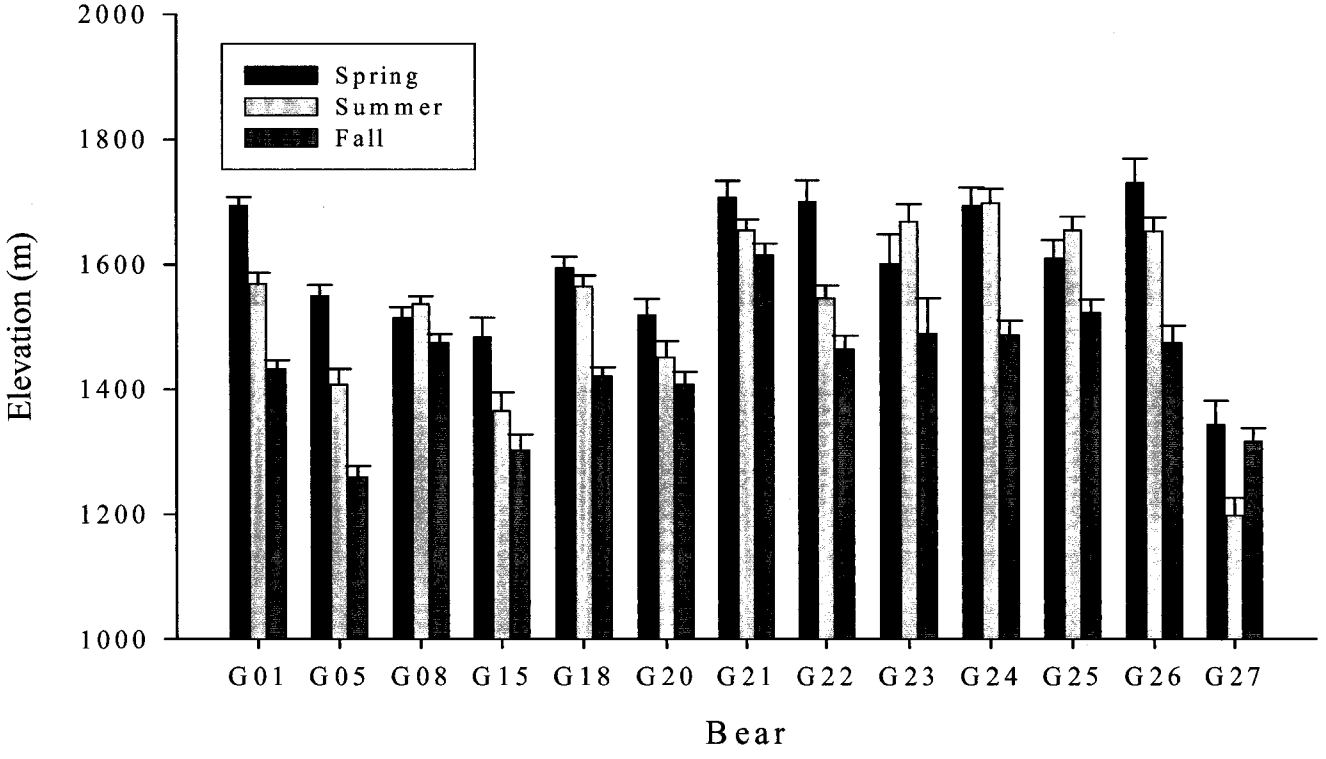

Figure 4.4. Mean elevations (± SE) used during spring (den emergence – 15 June), summer (16 June – 15 August), and fall (16 August – denning) by 13 female grizzly bears in the Besa-Prophet study area of northern British Columbia, 2001-2004.

alpine-type habitats (alpine shrub, non-vegetated, open alpine) more than 40 % of the time. The use of alpine shrub communities increased for 9 bears during the summer, with 6 of these bears having >30 % of their locations in this habitat class. Highest use of conifer stands tended to occur in fall, and 11 grizzly bears also increased their use of shrub communities during fall. The use of burn habitat classes was variable. Five grizzly bears increased their use of *Elymus* burns during the spring and 5 increased their use of this habitat during the fall.

Amongst other landscape features (Table 4.3), grizzly bears used moderate to high habitat diversity areas, as measured by fragmentation, in >80 % of each individual's locations in 32/39 bear seasons (13 individuals x 3 seasons); in ~50 % of the bear seasons, most use was in high-fragmentation areas. All bears predominantly used east or south aspects during the spring. Seven grizzly bears increased their use of north aspects during the summer months, and 3 increased their use of north aspects during the fall. Grizzly bear use of west aspects was <20 % of locations in 30 of 39 bear seasons.

Seasonal Selection

With 3 exceptions (variables associated with NDVI), habitat class was prevalent in all the top-ranked models across seasons for all individuals (n = 39 individual by season combinations) (Appendix C, Table C4). Additional variables included aspect (32/39 cases), fragmentation (26/39), elevation (21/39 cases), and slope (17/39 cases). Model averaging was required in all but 5 cases, with the number of models in an average set per individual ranging from 2 to 9. In 22 of the 34 seasonal cases that required averaging, the top model had a weight (w_i) greater than twice that of the second ranked model. Model performance

as estimated by Spearman's rank correlation (r_s) was high overall, ranging from 0.70 to 0.95 in all but 3 cases.

Because selection coefficients were similar in sign across years and individual grizzly bears inhabited the same home range each year, I pooled seasonal data for each individual across years for each season. Limited years of data precluded in-depth assessments of annual variation. Grizzly bears showed seasonal variation in their selection patterns for habitat class (Table 4.4) and other landscape features (Table 4.5) within their home range. Elevation was significant in 19 of 39 bear seasons overall. As a quadratic function, the opposite sign on each of the terms (+ elevation, - elevation^2) results in a bell-shaped curve, suggesting selection for a broad range of mid-elevation areas, i.e., bears select for higher elevations, but demonstrate strong avoidance of the highest elevations.

In the spring, there were few consistencies in selection patterns among individuals. Conifer stands (4/13 individuals) and high-biomass areas (5/13) were the habitat features most avoided by grizzly bears. Burned areas (5/13) and relatively complex habitats (as measured by medium or high fragmentation, 7/13) were the most selected categories during the spring. Six grizzly bears selected south aspects (1 avoided those aspects) and 4 grizzly bears avoided north aspects.

In summer, grizzly bears showed selection patterns similar to spring. Numerous habitat classes tended to be avoided, such as non-vegetated (11/13), conifer (9/13), and open alpine areas (9/13). Alternatively, grizzly bears tended to select for alpine shrub areas (8/13), and burned classes (11/13). Of the latter, 6 grizzly bears strongly selected for both burn cover types (Deciduous and *Elymus*). Models incorporating selection values for prey were important for only 1 bear, but the selection coefficients were not significant. In

contrast to spring, 7 grizzly bears selected north-facing slopes during the summer (1 avoided), and 5 grizzly bears significantly avoided south-facing slopes.

In fall, selection patterns were more variable. Some grizzly bears continued to avoid conifer (7/13) and non-vegetated (5/13) classes and selected burned areas (7/13). Alpine shrub areas were selected by 4 grizzly bears, but avoided by 2, whereas open alpine areas were selected by 1 grizzly bear and avoided by 5. Elevation was a significant component in most of the fall bear models (10/13). Grizzly bears did not appear to respond to aspect classes during the fall as only 13 of 65 total cases (5 aspect categories for each of 13 grizzly bears) resulted in either selection or avoidance for a particular aspect class. Similarly for fragmentation, only 6 of 39 cases had significant coefficients.

Selection coefficients in the seasonal layers for prey selection value can be found from the following sources: moose (Gillingham and Parker 2008a), elk (MKMA Conservation Area Design (Heinemeyer et al. 2004a, b), caribou (Gustine 2005; Gustine et al. 2006b), Stone's sheep (Walker 2005; Walker et al. 2007). Some grizzly bears appeared to respond to the selection values for different prey species in some years (Table 4.6). Prey selection values were included in the top 95 % model sets of 10 grizzly bears across the 3 seasons. Not all coefficients were significant in the final averaged models, but some patterns emerged. Some grizzly bears tended to select habitats ranked as high selection value for Stone's sheep during spring, and others for habitats ranked as high value for moose during summer. Individual bears were more variable in the fall with some selection for high-value habitats for all ungulate species, and some avoidance of high-value habitats for caribou and Stone's sheep.

Table 4.6. Resource selection function coefficients ($\beta_i \pm$ SE) representing seasonal selection patterns by individual female grizzly bears for areas of high selection value to available ungulate prey species in the Besa-Prophet study area of northern British Columbia. Coefficients are based on yearly data between 2001 and 2004, and only for those bears for which the prey-based models were ranked amongst the top 95 % model set as determined by AIC weights. Values in bold indicate significant selection (positive values) or avoidance (negative values) as determined by 95 % confidence intervals.

Season	Bear	Year	High Ungulate Selection Value			
			Moose	Elk	Caribou	Sheep
Spring	**G01**	2003	-0.24 ± 0.50	5.53 ± 3.79	-0.39 ± 0.54	**4.18 ± 2.07**
	G15	2003			1.67 ± 1.37	0.07 ± 0.12
	G18	2003			**1.24 ± 0.53**	**0.88 ± 0.39**
		2004	0.38 ± 0.23	**7.55 ± 0.64**	0.37 ± 0.25	**6.33 ± 0.42**
Summer	**G08**	2001	**1.63 ± 0.75**	-0.006 ± 0.03		
		2002	**8.08 ± 1.62**	-0.45 ± 0.38	0.98 ± 0.72	-0.51 ± 0.80
	G22	2002	**6.90 ± 1.32**	-0.34 ± 0.59	0.18 ± 0.35	-0.70 ± 0.92
		2003	2.13 ± 1.13	0.36 ± 0.34	0.39 ± 0.40	0.21 ± 0.58
	G27	2003	1.01 ± 0.80	-0.37 ± 0.30	-1.22 ± 0.81	-0.82 ± 0.64
Fall	**G20**	Pool	0.16 ± 0.09	0.02 ± 0.02	-0.10 ± 0.06	-0.002 ± 0.01
	G24	2003	-1.19 ± 0.87	-0.82 ± 0.58	**2.83 ± 0.97**	**-5.47 ± 1.21**
	G25	2002	**2.74 ± 0.88**	**1.79 ± 0.52**	**-2.45 ± 0.82**	**1.89 ± 0.64**
	G26	2004	5.78 ± 3.50	0.33 ± 0.44	-3.25 ± 2.07	1.08 ± 0.85

Discussion

Throughout their range in North America, grizzly bears occupy a broad range of habitat types to satisfy their security, thermal, and nutritional requirements. In this study, I documented seasonal variation in habitat use and selection by grizzly bears in the northern Rocky Mountains of BC. The BP provided an opportunity to investigate the ecology of northern interior grizzly bears in a region relatively free of human disturbance. Similar to the Flathead River drainage of southeastern BC (McLellan and Hovey 2001), grizzly bears in the BP are currently free to roam among habitats in both mountainous terrain and wide valleys, unlike many other populations where habitat use has been restricted because of fragmentation associated with agriculture, hydroelectric reservoirs, forestry, and settlement (Servheen 1983; Zager et al. 1983; Wielgus and Bunnell 1994; Waller and Mace 1997). In the coming years, however, grizzly bears in the northern Rocky Mountains likely will face increased pressure from forestry, mining, and oil and gas exploration and development.

My study highlights that the management and conservation of grizzly bears must be specific to each population (or minimally to each region). The observation that grizzly bears were found at higher elevations during the spring is counter to what has been typically reported for grizzly bears. In the Swan Mountains in northwestern Montana and Yellowstone National Park in Wyoming, for example, grizzly bears showed strong patterns of seasonal elevational movements, typified by movements to lower elevations during the spring to exploit foods not available at higher elevations (Boyce and Waller 2003). Other populations have shown similar trends: Glacier National Park, MT (Martinka 1972), Jasper National Park, AB (Mundy and Flook 1972; Nielsen et al. 2002), Yellowstone National Park, WY (Mealey 1980), Mission Mountains, MT (Servheen 1981), Denali National Park,

AK (Stelmock and Dean 1986; Darling 1989), Swan Mountains, MT (Waller and Mace 1997; Mace et al. 1999), Yellowhead region of west-central BC (Nielsen et al. 2002), interior BC (Ciarniello 2006). In the Flathead River drainage of Montana, most bears were observed to be elevational migrators that moved to riparian areas shortly after den emergence in the spring, although some bears were mountain residents that remained at high elevations following spring emergence where they selected avalanche chutes (McLellan and Hovey 2001).

The majority of female grizzly bears in the BP remained at relatively high elevations throughout the spring and summer seasons, although they were found over a broader range of elevations during the summer. Use of a broader range of elevations during the summer has been documented elsewhere (Mace et al. 1999). During this study, alpine areas were snow-free early in the spring and feeding by grizzly bears in the alpine zones appeared focused on graminoids, and roots of *Astragalus* sp. and *Oxytropis* sp. I observed 2 bears attempting to chase down elk herds gathered in high-elevation meadows. In Banff National Park, early-season feeding on yellow *Hedysarum* roots, bearberries (*Arctostaphylos uva-ursi*), and graminoids occurred at relatively high elevations (>1900 m) in dry, steep meadows (Hamer and Herrero 1987). As the season progressed, some bears remained in these high elevation meadows and others migrated to the valley bottoms, a pattern also observed for grizzly bears in Waterton Lakes National Park, AB (Hamer et al. 1991). Several other studies have reported that family groups, especially cub families, chose more rugged, isolated terrain than lone bears (Pearson 1975; Sharafutdinov and Korotkov 1976; Stelmock 1981) and were found at higher elevations (Russell et al. 1979; Glenn and Miller 1980) with smaller home ranges and restricted movements related to security rather than

feeding (Dahle and Swenson 2003a; Suring et al. 2006). Eleven of the BP grizzly bears had cubs of the year or yearling families during the course of this study (1 with a single cub, 8 with twins, and 2 with triplets), and seasonal range sizes and movement rates were linked to whether sows were accompanied by cubs of the year (see Chapter 2).

Elevation was a significant variable in both individual and global selection models for grizzly bears in the BP, which is likely due to both specific habitat associations with elevation (e.g., alpine shrub) and security cover that can be found at higher elevations but that might be of poorer habitat quality (e.g., talus slopes). These models also included various landscape features and 10 habitat classes believed to be important to the ecology of grizzly bears. Many of these models were averaged, and although model averaging provides more robust coefficients, it tends to inflate standard errors that may impact inferences (Burnham and Anderson 2002). This would be of greatest concern relative to models derived from small sample sizes that have inherently higher variances, as is the case with spring data for many bears. The strongest patterns of selection or avoidance were during the summer season.

As individuals, bears were relatively consistent in their selection of habitat classes across years and among seasons. There was more variability in selection among individual bears, but general consistencies still emerged. Burn-type habitats were important to bears year round. Both the *Elymus*- (younger disturbance) and deciduous-dominated (older disturbance) burn categories include prescribed and natural fires, and other disturbed areas such as avalanche chutes that are similarly characterized by high productivity and low-stature vegetation that is distinct in composition from wet and dry alpine areas, transition areas, and the shrub habitat types. The importance of avalanche chutes appears ubiquitous

to all alpine bear populations (e.g., Ramcharita 2000). I was unable to quantify their relative importance in the BP, however, because these productive areas could not be distinguished spectrally from the burn habitat categories (Lay 2005), and their extent in the BP may be limited. Numerous studies have documented the importance of wildfires in the abundance and distribution of various bear foods, and the subsequent seasonal or annual importance of these areas to local bear populations (Zager et al. 1983; Hamer and Herrero 1987; McLellan and Hovey 2001). Prescribed burning has been recommended as a silvicultural treatment for grizzly bear foods that are negatively impacted by forestry activities (Nielsen et al. 2004). Prescribed burning began in the 1980's and continues today in the BP to expand habitats and population sizes of elk and Stone's sheep (R. Woods, pers. comm., BC Ministry of Environment). Young regenerating stands contain greater abundances of most critical bear foods including ungulates, green herbaceous vegetation, roots, and other subterranean foods (Martin 1983; Zager et al. 1983; Irwin and Hammond 1985; Knight 1999). Similarly, the selection of shrub habitats by bears in the summer and fall may be related to both foraging and ungulate encounters.

The greenness band derived from tasseled-cap transformations of TM satellite imagery has been found to be a powerful indicator of grizzly bear habitat (Mace et al. 1998, 1999; Carroll et al. 2001b; Nielsen et al. 2002; Boyce and Waller 2003). Habitats with high greenness values include avalanche chutes, shrub lands, cut blocks, and riparian areas with high canopy cover of deciduous shrubs (Waller and Mace 1997). Greenness has typically been used as a surrogate for vegetation quantity and quality (Cihlar et al. 1991; White et al. 1997), and is highly correlated with leaf-area index (White et al. 1997; Boyce and Waller 2003), although there is little information as to what greenness actually represents beyond

these attributes (White et al. 1997). Mace et al. (1999) did not find any relationships between greenness, vegetation species composition, and physiography.

Greenness is highly correlated with NDVI (Tucker and Sellers 1986; Ruimy et al. 1994; Oindo 2002), my surrogate for vegetation biomass (absolute NDVI) and quality (change in NDVI over time). I chose to use NDVI over greenness because I felt that NDVI values may have a more direct biological link to phenological processes occurring across the landscape to which grizzly bears respond. In my study, models incorporating habitat class consistently outperformed those based on attributes related to NDVI. The utility of the greenness index in predicting grizzly bear occurrence appears restricted to populations that are primarily herbivorous (Mace et al. 1999; Boyce and Waller 2003), and the use of NDVI may have the same limitations. Furthermore, both greenness and NDVI may be limited in some management applications because high values can be obtained for different habitat types that are functionally diverse (e.g., conifer stands vs. productive avalanche chutes vs. wetland meadows) (Apps et al. 2004), and may vary by season. Despite this potential limitation, NDVI values in the BP were strongly influenced by understory vegetation. Burned and shrub habitat classes in summer had much higher NDVI values than conifer stands because the majority of the NDVI value is attributed to understory vegetation (Lay 2005).

It has been concluded elsewhere that the greenness index would be least effective where grizzly bear foraging was not related to vegetation (Mattsen et al. 1991a,b; Boyce and Waller 2003). Grizzly bears in the BP are opportunistic omnivores, with females obtaining as much as 50 % of their protein intake from meat (Chapter 5), depending on the season. In addition, the availability of plant foods in the BP that are generally favored by grizzly bears

appears less diverse than that of other southern Rocky Mountain habitats (e.g., Nielsen et al. 2003). The moderate home-range sizes, high degree of home range overlap, and high reproductive output and cub survival of grizzly bears in the BP, however, are indicative of high quality habitats overall (see Chapter 2) and support the premise that the abundance of plant foods that are available, in combination with high ungulate densities, sustain this population. In areas immediately south of my study area (between Nevis Creek and Sikanni Chief River areas), McCrory (2003) observed spring and summer feeding areas that contained mainly cow-parsnip (*Heracleum lanatum*), horsetail (*Equisetum* spp.), grasses, and sedges (*Caryx* spp.). Berry-producing areas (kinnikinnick, *Arctostaphylos uva-ursi,* and soopolallie, *Shepherdia canadensis*) were found in burned areas, drier slopes, and in river breaks. Root/corm feeding sites were uncommon. Given the variability in prey consumption by grizzly bears in the BP, it is not surprising that selection models based on attributes associated with NDVI were not ranked highest. This is not to discount the importance of vegetative features to grizzly bears, but rather demonstrates that habitat class, combined with topography and physiographic features, may be better predictors of the distribution of a large omnivore with a varied diet because these features influence not only the availability of plant foods, but also determine the likelihood of encountering ungulate prey.

I related resource selection by grizzly bears to potential 'prey benefit' surfaces for each of the major available ungulate prey. The potential of grizzly bears as effective predators and scavengers of ungulates has been well documented, and some of my model results in individual years are consistent with dietary information obtained through stable isotope analysis (see Chapter 5). Of the bears analyzed for habitat selection, I had dietary

information obtained from stable isotopes for 5 of them (G01, G15, G18, G26, and G27), and the prey benefit surface was important to each of these bears. These findings are consistent with my stable isotope analyses, which indicated that these animals in particular consume 31 -51% meat protein across seasons. Some individual bears appear to respond to annual shifts in the abundance and distribution of ungulate prey in the BP. Selection of Stone's sheep habitat during the spring by some individuals in some years, for example, probably resulted from significant overlap of ranges when grizzly bears used similar high-elevation habitats rather than a particular predation strategy (estimates of the proportion of Stone's sheep in the diets of grizzly bears was consistently low; Chapter 5). During the summer, selection of high-quality moose habitat by some grizzly bears corresponded with my observations of high levels of use and consistent selection of both burn and shrub cover classes.

Approaches to habitat modeling that utilize remote-sensing data, animal radio-telemetry locations, and analyses of habitat selection are powerful tools in examining patterns of wildlife distributions (Mace et al. 1996, 1999; Boyce and Waller 2003; Apps et al. 2004). Nonetheless, there are several important limitations and considerations for my study. Inferences drawn from analyses of resource selection should be tempered with examinations of relative habitat use, as I have presented in Tables 4.2 and 4.3. For example, grizzly bears in the BP consistently avoided dense spruce and pine stands (conifer class), which averaged approximately 16% of annual ranges. For some female grizzly bears and depending on the season, up to 1/3 of their locations in the BP were in conifer stands (in these cases, up to 37 % of the seasonal range was conifer). Other studies have reported either avoidance (Blanchard 1983; Aune 1994) or selection for forest types (Servheen 1981;

Almack 1985). In the Swan Mountains, the closed-canopy forest cover type was least selected, but accounted for 62 % of the study area and about 50 % of all telemetry locations were in this cover type (Waller and Mace 1997). Forest cover likely contains resources important to grizzly bears, such as nutritional value or thermal and security properties (Suring et al. 2006).

Biases in the acquisition success of GPS collars associated with different cover types, topography, and animal behaviour may influence model inferences (D'Eon et al. 2002; Frair et al. 2004; Cain et al. 2005; DeCesare et al. 2005; Graves and Waller 2006). I was unable to correct for habitat and terrain-induced GPS-collar bias by using sampling weights (e.g., Nielsen et al. 2002) for grizzly bear locations because I did not have local models predicting GPS fix acquisition as a function of terrain and land-cover characteristics (see Frair et al. 2004). Nonetheless, these biases were probably relatively low given the distribution of open habitat classes covered >60 % of annual and seasonal ranges of grizzly bears in the BP. There appears to be a behavioural component to collar fix acquisition. Resting position and canopy cover interact, resulting in lower fix rates (Heard et al. 2008). Individual collars in the BP were variable, but on average fix success was lowest at 0100 when bears are expected to be least active. RSF coefficients should be interpreted with caution (Frair et al. 2004). Given the distribution of open habitat classes, however, I believe that the observed seasonal elevational differences and associated changes in patterns of habitat use and selection by grizzly bears were driven primarily by biological mechanisms.

The potential for resource exploration and development in the BP area of northern BC necessitates the development of sound management plans that include baseline information on how grizzly bears interact with the landscape. Prescribed burns are selected

by grizzly bears in the BP, and the current regime using prescribed fire to manage elk and Stone's sheep may benefit the population of grizzly bears in terms of vegetative characteristics and access to ungulate prey. Avalanche chutes, which could not be detected separately from burned disturbed areas via satellite imagery, are probably important, as reported in other studies. Shrub-cover types in the BP provide both high-quality forage and potential encounters with ungulate prey. If there is future development in the area, the need for secure forested cover types may increase in importance.

Management directives should plan development in a manner that enables access to targeted resources while conserving habitat values for grizzly bears. Because grizzly bears require a wide range of habitat types across elevational gradients to meet nutritional, thermal, and security requirements, maintaining this variability across the landscape will be the management challenge for this region. My focus on habitat use and selection by female grizzly bears is an important baseline for grizzly bear ecology in the northern Rocky Mountains.

Chapter 5: The Use of Stable Isotopes of Carbon and Nitrogen to Infer Large-Mammal Predator-Prey Relationships

Introduction

Few studies have attempted to examine broad-scale ecosystem level dynamics of multi-predator multi-prey systems, yet intact systems still exist where large carnivores are considered to be dominant factors in ungulate dynamics (Kunkel and Pletscher 1999; Husseman et al. 2003; Radloff and du Toit 2004). Large mammal predator-prey research in North America has tended to focus on two scenarios. First is that of a single predator regulating a single prey population, such as wolves (*Canis lupus*) and moose (*Alces alces*) in British Columbia (Bergerud et al. 1983; Bergerud and Elliott 1986), on Michigan's Isle Royale (Post et al. 2002; Vucetich et al. 2002) and in Yukon (Hayes and Harestad 2000). Numerous models have attempted to explain and predict the functional (changes in kill rates) and numerical (changes in density) responses of the predator population and its preferred prey (reviewed by Messier 1994, 1995). Second is the capacity of a single predator to regulate or structure a multi-prey community (Dale et al. 1994, 1995; Bergerud and Elliott 1998; Lingle 2002), or potentially entire ecosystems (Smith et al. 2003; Ripple and Beschta 2004).

The relationships among major sources of mortality, such as food limitation, competition, predation, and density-dependant changes in key demographic parameters of ungulate populations, have been difficult to document (Messier 1989). In complex systems, however, an understanding of the interactions between numerous predators with potentially overlapping resources is vital to developing sound conservation and management strategies.

In northern North America, wolves and bears (*Ursus sp.*) are the primary predators considered to be in sufficient numbers to potentially limit and regulate ungulate populations.

Wolves are typically opportunistic predators with diverse diets, although cervids are preferred prey in both Europe and North America (Okarma 1995; Spaulding et al. 1998). Several factors can affect selectivity by wolves for large prey items, such as availability and profitability of prey types, the degree of habitat overlap between predator and prey, risk of injury, probability of successful capture, and encounter rate (Huggard 1993). Where numerous large prey species are available, wolves have been shown to target those that are smaller and easiest to catch (Mech 1970; Dale et al. 1995; Forbes and Theberge 1996). Wolves readily switch between ungulate prey species in response to shifts in ungulate abundance or ungulate migration (Ballard et al. 1997), but seasonal variation in prey consumption may decrease with increasing availability of large wild herbivores (Meriggi et al. 1996). During periods of ungulate decline, alternative prey items can be locally or seasonally important (Spaulding et al. 1998). Additionally, wolves may exhibit prey selection at different scales, choosing home ranges that provide predictable prey encounters over the long term, and selecting prey with the highest profitability within these ranges (Kunkel et al. 2004).

Grizzly bears (*U. arctos*) are known both as terrestrial scavengers and predators (Green et al. 1997; Mattson 1997). Predation by both black (*U. americanus*) and grizzly bears on ungulate calves potentially can regulate ungulate populations at low densities (Reynolds and Garner 1987; Boertje, et al. 1988; Larsen et al. 1989; Ballard et al. 1991; Schwarz and Franzmann 1991; Gasaway et al. 1992). The use of ungulates by grizzly bears varies by season and area, and depends on ungulate density (Mattson 1997). Although

seasonal variation in bear diets has been well documented (Servheen 1983), how the use of ungulates and rates of predation vary with shifts in the composition of ungulate species, spatial and temporal variation in ungulate distributions and densities, and the availability of alternate food resources (e.g., vegetation) remains unclear (Mattson 1997). Differences in ungulate use between male and female (Ballard et al. 1982; Reynolds and Garner 1987; Boertje et al. 1988; Mattson 1997), and between adult and sub-adult grizzly bears (Young and McCabe 1997) have been documented. Reasons for significant meat intake by grizzly bears have been proposed (Hilderbrand et al. 1999a), and when combined with demonstrated constraints associated with an herbaceous diet (Rode et al., 2001), they support the conclusion that males are more carnivorous than females, which allows the nutritional opportunity for sexual dimorphism in size (Hilderbrand et al. 1998; Jacoby et al. 1999).

Past studies of carnivore diets generally have been limited in their estimates of kill rates and prey selection by winter backtracking to kill sites (Smith et al. 2004). A majority of other studies have utilized scat analyses to estimate the proportion of prey items in the diet, but these methods can be biased by differential digestibility of prey items (Roth and Hobson 2000). Advances in stable-isotope ecology now allow better estimates of the dietary contribution of different prey species to predator dynamics, and contribute to a better understanding of the structure and dynamics of ecological communities (Kelly 2000; Post 2002; McCutchan et al. 2003). Stable-isotope techniques have the potential to provide a more accurate measure of trophic position and to capture complex interactions such as omnivory, because they can track and integrate the assimilation of energy or mass flow through trophic pathways and ecological communities (Post 2002).

Stable N isotopes reflect the trophic position of an organism within a food web because the ratio ($^{15}N/^{14}N$ or $\delta^{15}N$) changes predictably with trophic level, owing mainly to the preferential assimilation of ^{15}N to body tissues and excretion of ^{14}N in urine (Peterson and Fry 1987). As a result, nitrogen ratios in a consumer are typically enriched by 3-5‰ relative to dietary nitrogen (Gannes et al. 1998). Although stable isotopes of carbon theoretically should change little with trophic position (DeNiro and Epstein 1978; Vogel 1978; Chisholm et al. 1982), more recent studies have shown highly variable carbon isotope ratios between trophic levels (Post 2002; McCutchan et al. 2003; Robbins et al. 2005). Carbon-isotope ratios in diet reconstructions reflect sources of primary productivity, and may distinguish between C3 browsers and C4 grazers (Ambrose and DeNiro 1986; Gannes et al. 1998). When combined with nitrogen-isotope ratios, they may identify niche partitioning among herbivores that overlap in habitat use but differ in diet selection (Stewart et al. 2003). Differences in the degree of herbivory and the contribution of different prey sources are subsequently reflected in the tissues of consumers, which is useful in reconstructing the proportion of various prey items in carnivore and omnivore diets (Ben-David et al. 1997). The more isotopically distinct the prey signatures, the better resolution obtained from mixing models used to evaluate predator diets (Ben-David et al. 1997; Phillips and Gregg 2003).

Ecologists are often interested in seasonal and/or annual variation in prey selection. Because the turnover rates of stable isotopes vary by tissue, dietary information over different time scales can be obtained by isotopic measurements of several tissues from the same individual (Tieszen et al. 1983; Hobson and Clark 1992a, 1992b). For example, muscle tissue and red blood cells provide dietary information from the previous 2-3 months,

whereas the plasma component of a blood sample provides dietary information over the past 10-14 days (Tieszen et al. 1983; Hobson and Clark 1992a, 1992b). Metabolically inert tissues such as feathers, hair, skin, and nails, do not turn over and, therefore, reflect the diet of an individual over the period that these tissues were grown (Roth and Hobson 2000). The ability to extract different types of information from a single individual is particularly useful in studies of animals that rely on, or switch between, seasonally abundant food sources (Roth and Hobson 2000).

Several types of models, including Euclidean distance and linear mixing, have been proposed to estimate the proportion of prey items in the diet of a consumer (Ben-David et al. 1997; Szepanski et al. 1999; Phillips 2001; Phillips and Koch 2002). Because distinct isotopic signatures generally persist for only 1 or 2 elements per system, dietary determinations often are limited to estimates for 2 or 3 sources (Phillips and Gregg 2003). In complex systems, however, the inclusion of a larger number of sources in diet reconstruction is often necessary. The IsoSource model (Phillips and Gregg 2003) is an extension of the standard linear mixing model. IsoSource generates a range of possible solutions for n isotopes and $> n+1$ sources that conserves mass balance with respect to combinations of estimated prey proportions accounting for the observed predator signature.

In northeastern British Columbia (BC), the "predator landscape" includes interactions between the major predators (bears and wolves) and a diverse ungulate community (elk *Cervus elaphus*, moose *Alces alces*, Stone's sheep *Ovis dalli stonei*, and caribou *Rangifer tarandus*). As part of my overall goal, this study quantified the food habits of grizzly bears and wolves using stable isotope analyses. A primary objective was to quantify the relative contribution of major prey types to the diets of wolves and grizzly

bears. I predicted high seasonal variability in prey selection by wolves and variability among packs because of heterogeneity in habitat and prey distribution, with highest within-pack variability (number of food types) during the summer period and more selectivity shown during the rest of the year. I predicted that meat should be the largest proportion of bear diets in early spring, when alternative high-protein sources are unavailable, as well as in fall, when a rapid increase in body mass is required prior to hibernation. Increases in lean body mass during spring provide the musculature and connective tissue to support later stores of body fat (Belant et al. 2006). Availability of high quality food in fall is critical to fat deposition for use during dormancy (Farley and Robbins 1995; Barboza et al. 1997; Belant et al. 2006). Protein intake in excess of nitrogen requirements may be able to be stored as lipids (Peltier and Barboza 2003), and bears have been shown to optimize the composition of gains in body mass (i.e., fat or lean body mass) when consuming mixed diets of varying protein content (Rode and Robbins 2000; Felicetti et al. 2003b). In order to maintain larger sizes, males are likely to consume more meat than females. Plant material should represent the largest proportion of the diets consumed by bears during the summer. A second objective was to compare diet composition as determined by stable isotopes with food habits determined from scat samples of wolves during the summer period.

My final objective was to assess the contribution of fractionation values to isotopic determinations of diet. The estimation of assimilated diet from stable isotopes depends on accurate estimates of the enrichment ('fractionation') occurring between the diet and tissue of the consumer (Robbins et al. 2005). Fractionation is related to the rates that isotopes undergo chemical reactions (Roth and Hobson 2000). The weakest link in the application of stable isotope analyses to dietary reconstructions relates to the estimation of appropriate

fractionation values (Phillips and Koch 2002). Following Phillips and Koch (2002) and Vanderklift and Ponsard (2003), I compared dietary estimates for wolves and grizzly bears using a range of documented fractionation values generated from studies on captive foxes (*Vulpes vulpes*) (Roth and Hobson 2000) and captive bears (Hilderbrand et al. 1996).

To this point in the thesis I have presented concurrent data on variations in the home-range sizes of wolves and grizzly bears, movement patterns of these predators, and how they use the landscape. This chapter is a significant component in examining the ecology of wolves and grizzly bears in the BP. Inferences on prey consumption may yield very different conclusions if based solely on analyses of resource selection. My study, therefore, is unique in the level of comprehensive data on concurrent resource use by multiple predators, and comparing that information on actual, rather than perceived, prey consumption. Stable-isotope analysis, in conjunction with RSFs, is a powerful tool to examine system-wide linkages. By looking at the relative contribution of different prey items in the diets of wolves and grizzly bears, as opposed to a general assessment of 'meat' or 'plant' eaters, and how prey consumption varies seasonally, in combination with resource use, we can better identify potential conservation priorities.

Study Area

The Muskwa-Kechika Management Area (MKMA) in northern BC covers approximately 6.4 million ha. The study occurred primarily in the 204,245 ha Besa-Prophet pre-tenure planning area (BP) and the 80,771 ha Redfern-Keily Provincial Park within the MKMA, as well as in portions of surrounding areas (Fig. 5.1). Three ecozones typify the

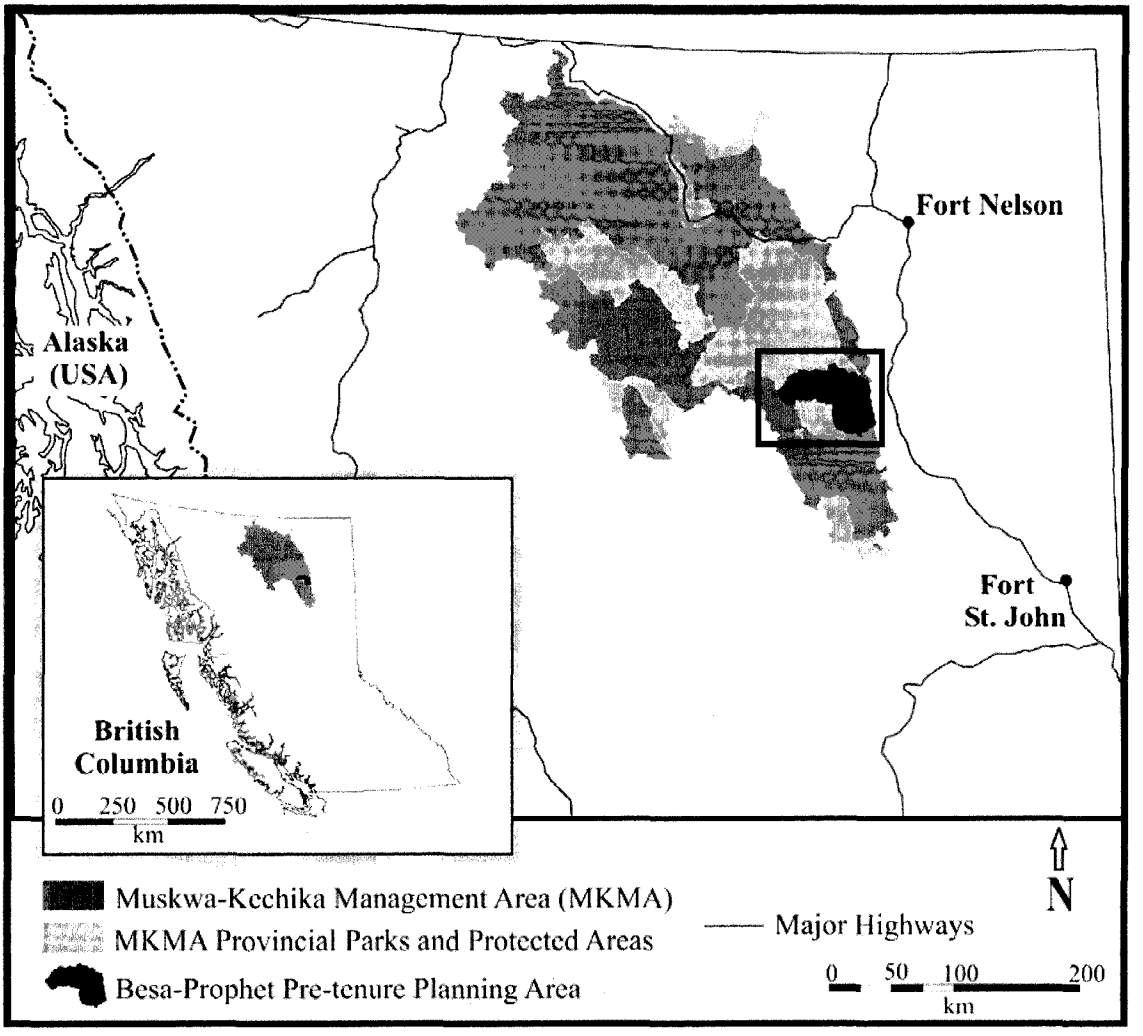

Figure 5.1. Study area in the Muskwa-Kechika Management Area (MKMA), northeastern BC.

region (Meidinger and Pojar 1991): the boreal zone characterized by white and black spruce (*Picea glauca* and *P. mariana*) at low elevations, subalpine areas characterized by spruce, willow (*Salix* sp.), and birch (*Betula glandulosa*), and alpine tundra. The topography is an interlaced network of north-south ridges and east-west valleys with a prominence of south-facing slopes. The BP supports one of the largest intact predator-prey ecosystems in North America. Ungulates include moose, elk, caribou, Stone's sheep, and mountain goats (*Oreamnos americanus*). Predators capable of preying on these ungulates include wolves, grizzly bears, black bears, cougars (*Felis concolor*), coyotes (*Canis latrans*), and wolverines (*Gulo gulo*), although it is believed that only wolves and grizzly bears are of sufficient numbers to be capable of potentially limiting or regulating ungulate communities.

Methods

Sample Collection for Stable Isotope Analysis

Most samples for isotopic analyses were obtained between November 2001 and February 2003 during animal capture/collaring activities as part of a larger study. Wolves were captured between December and March 2001-2003, and bears were captured between May and June 2001-2003. Blood and guard hair samples were collected from both species. Additional bear hair samples were obtained from a DNA mark-recapture study conducted in the same area (Poole et al. 1999). I subsequently sectioned bear hairs into thirds where the tip portion of the hair is representative of the spring diet (May/June), the mid-section representative of summer (July/August), and the root portion representative of fall (September/October), assuming constant growth rates of hairs (Jacoby et al. 1999).

Stable isotope analysis requires that baseline prey signatures are established. Hair and blood samples were collected from 50 caribou (November to February) and 15 moose (March). Hair samples were collected from 36 Stone's sheep (December to January). Additional hair and meat samples from moose and elk were obtained from guide outfitters (August to October). Some moose and elk hairs were sectioned in half to provide dietary estimates for spring/early summer. I also analyzed tissue from beaver (*Castor canadensis*) from a nearby area.

Blood samples were centrifuged for 5 min within 2 hr of collection, and plasma was pipetted into separate vials. All blood, plasma, and meat tissues were kept frozen until processing for stable isotope analysis. Blood samples were freeze-dried and homogenized. Muscle tissue (meat) was washed in distilled water, freeze-dried, and ground into a fine powder (Ben-David et al. 1997; Hobson et al. 2000). Because variations in lipid concentration can significantly influence measurements of carbon isotope ratios (Rau et al. 1992), lipids were extracted from muscle tissue by a modified Bligh and Dyer (1959) technique with chloroform as the solvent (as described by Pinnegar and Polunin 1999). Hairs were cleaned of surface oils in a 2:1 chloroform:methanol solution, rinsed with distilled water, and air-dried (Hobson et al. 2000).

Plants assumed to be important in the diets of bears based on Ciarniello et al. (2002a, b) were collected opportunistically between 1000 m and 2000 m elevation. These included above-ground foliage from *Festuca* sp., *Carex* sp., *Elymus* sp., *Equisetum* sp., *Epilobium angustifolium, Heracleum maximum*, and roots and bulbs of *H. maximum, Hedysarum* sp., *Astragalus* sp., and *Oxytropis* sp. Plant material was dried at 60 °C for 48

hr and ground to a fine powder using a Thomas-Wiley mill (Swedesboro, NJ) with a 0.5-mm sieve screen.

Sub-samples (1 mg of blood, muscle, and hair tissues; 2.5-3 mg of plants for dual measurement of C and N signatures) were weighed into miniature tin-cups (5x8 mm) (Costech Analytical Technologies Inc., Valencia, CA, USA) for combustion. Stable-isotope ratios of carbon and nitrogen were measured on a continuous flow isotope-ratio mass spectrometer in the Stable Isotope Facility at the University of California Davis. Stable-isotopes are expressed in delta notation (δ) in parts per thousand (‰) in the form:

[1] $$\delta X = ((R_{sample}/R_{standard}) - 1) \times 10^3$$

where X is ^{13}C or ^{15}N and R_{sample} and $R_{standard}$ are the corresponding ratios of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and standard, respectively (Peterson and Fry 1987). The standards are Pee Dee Belemnite (PDB) for ^{13}C and atmospheric N_2 for ^{15}N.

Dietary Determination by Isotopes

I used a K nearest-neighbor randomization test with Bonferroni correction to determine whether stable isotope ratios of prey types were significantly different (Rosing et al. 1998). This test treats $\delta^{13}C$ and $\delta^{15}N$ values as spatial data. To estimate the proportions of prey items in the diets of wolves and grizzly bears, I used the IsoSource model described by Phillips and Gregg (2003). All possible combinations of each source contribution (0-100%) towards the observed predator signatures were examined in small increments (1%). Feasible solutions included those combinations that were within 0.1‰ tolerance of the observed signatures for both $\delta^{13}C$ and $\delta^{15}N$. Signatures from individual wolves in the same pack were averaged to obtain a 'pack' signature. Bear models were run individually, and

average signatures were used to obtain population level estimates for meat and plant consumption based on the assumed relationship:

[2] $$P_a = [(\delta^{15}N_{hair} - 4.76)/0.91 - \delta^{15}N_p] / (\delta^{15}N_{hair} - \delta^{15}N_p)$$

where P_a is the proportion of animal protein in the diet, $\delta^{15}N_{hair}$ is the nitrogen signature of the bear hair, and $\delta^{15}N_p$ is the baseline plant nitrogen signature (Hobson et al. 2000).

Mean fractionation values for the bear models were determined from regression equations generated from captive bears fed a constant diet (Hilderbrand et al. 1996), and values for wolf models from a study on captive red foxes (*Vulpes vulpes*) (Roth and Hobson 2000) were deemed most appropriate (Urton and Hobson 2005). A range of feasible fractionation values around these means was generated from the captive studies and from other mammalian studies in the literature (Ben-David et al. 1997; Post 2002; Robbins et al. 2005). I assumed no difference in diet-tissue fractionation between forage and the different herbivore tissues (blood, meat, hair) used in the seasonal models (Tieszen and Boutton 1988; Hobson 1995; Urton and Hobson 2005). I report mean prey composition in the diets of wolves and grizzly bears based on the mean fractionation values. Uncertainty in my dietary estimates is reported as the full range of prey proportions generated from the range of feasible solutions.

Dietary signatures were determined for 4 seasons for wolves based on available samples (not 5 as in previous habitat analyses). The wolf seasons were winter (January and February corresponding to breeding and peak snow depth), early spring (March and April, corresponding to the pre-denning period), summer (including the denning period from May through July and the late-summer rendezvous period from August through September, when pups travel with the pack but are not yet fully grown), and fall (October to December,

corresponding to the period when pups are almost fully grown and traveling with the pack). There were 3 seasons for grizzly bears based on plant phenology. The bear seasons were spring (mid-April to 15 June, den emergence to the beginning of plant green-up), summer (16 June to 15 August, start of plant green-up to start of senescence, and fall (16 August to 31 October, beginning of plant senescence to denning).

From the prey species, I selected the hair, tissue, or blood sample that most appropriately indexed the within-season diet composition of wolves (Table 5.1) and bears (Table 5.2). The range in feasible fractionation values used in the predator diet composition models is presented in Table 5.3.

Dietary Determination by Scat Analysis

Wolf dens were located from fixes downloaded from animals with global positioning satellite (GPS) collars. Wolves in the BP den typically between mid-May and late July. Scat samples were collected near den sites in early August. Fecal samples (n = 345) were air dried in the field, and subsequently sent to C. Conroy (Kimberly, BC) for processing and dietary analysis. To prevent parasite transmission during processing, scats were autoclaved at 15 psi and 120°C for 20 min before washing in warm water and detergent to remove dirt, oils, and unidentifiable materials. Some hairs required further cleaning with acetone to remove adhering oils or dirt. After being air dried, each sample was examined for hair, tooth, bone, and feather remains.

Mammals were identified using 4-10 representative guard hairs with tip and base intact (Kennedy and Carbyn 1981). Microscopic characteristics of scale patterns and medulla traits, and macroscopic color banding patterns were compared to reference hairs obtained from live and deceased animals, and museum skins of known prey species.

Table 5.1. Isotopic signatures of prey used in diet composition models for wolves by season in the Besa Prophet area, northeastern British Columbia, 2002-2003. rbc indicates red blood cells.

Prey	Sample	δ13C	δ15N	Winter	Early Spring	Summer	Fall
Elk	Hair	-24.42	2.41			√	
	Meat	-24.68	3.12	√	√		√
Sheep	Hair	-23.75	2.81	√	√	√	√
Caribou	rbc 2001	-23.28	2.77				√
	rbc 2003	-23.02	1.96	√	√		
	Hair 2003	-23.14	2.46			√	
Moose	Hair (whole)	-24.47	1.53			√	
	rbc	-24.67	0.61	√	√		
	Meat	-24.39	1.58				√
Beaver	Meat	-25.01	1.43				
	Hair	-24.04	2.38				

Table 5.2. Isotopic signatures of prey used in diet composition models for grizzly bears by season in the Besa Prophet area, northeastern British Columbia. rbc denotes red blood cells.

Prey	Sample	δC	δN	Spring	Summer	Fall
Elk	Hair	-24.42	2.41		√	
	Meat	-24.68	3.12			√
Grazers (sheep, elk)	Hair	-24.03	2.73	√		
Sheep	Hair	-23.75	2.81		√	√
Caribou	rbc 2001	-23.28	2.77			√
	Hair 2003	-23.14	2.46	√	√	
Moose	Hair (whole)	-24.47	1.53		√	
	Hair (tips)	-23.93	1.27	√		
	Meat	-24.39	1.58			√
Beaver	Meat	-25.01	1.43			
	Hair	-24.04	2.38			
Plants	Roots and leaves	-26.94	-1.85	√	√	√

Table 5.3. Means and ranges of N and C fractionation values used in isotopic estimates of diet composition for grizzly bears and wolves. Mean values for bears were generated from regressions in Hilderbrand et al. (1996) and the ranges from Ben-David et al. (1997) and Post (2002). All fractionation values for the wolf models were from captive fox studies (Roth and Hobson 2000).

Species	Sample	ΔN		ΔC	
		mean (‰)	range (‰)	mean (‰)	range (‰)
Bears	guard hairs	4.5	3.0 - 5.0	3.9	2.0 - 4.2
Wolves	rbc	2.6	2.6 - 3.6	0.6	0.6 - 1.2
	plasma	4.2	4.0 - 4.4	0.6	0.6 - 1.2
	guard hairs	3.3	3.1 - 3.5	2.6	2.0 - 2.6

Identification keys from Adorjan and Kolenosky (1969) and Kennedy and Carbyn (1981) were used as additional aids. Scat results are presented as percent occurrence (the number of fecal samples containing a particular prey item relative to the total number of fecal samples).

Results

Prey Signatures

In the wolf models, $\delta^{13}C$ values ranged from a low of -25.00‰ (beaver) to -23.02‰ (caribou), and $\delta^{15}N$ values from 0.61‰ (moose) to 3.12‰ (elk). In the bear models, $\delta^{13}C$ values ranged from -26.94‰ (plants) to -23.14‰ (caribou) and $\delta^{15}N$ values from -1.85‰ (plants) to 3.12‰ (elk). Prey isotopic signatures were significantly different within each wolf and bear season (winter, spring, fall: $P < 0.001$; summer: $P < 0.013$), except for bears in spring when elk and sheep ($P = 0.12$) were pooled into a grazer category.

Wolves

All packs consumed large amounts of elk (38-89%) in winter (Table 5.4). Diets of western (Dopp/Keily, Richards/Prophet) and central (Nevis) packs also contained large contributions from Stone's sheep, which continued to be an important prey (38-59%) item in the spring. In winter 2003, members of the Richards pack vacated their territory and occupied a new home range further to the northwest, and were renamed the Prophet pack. With that change, a larger portion (48%) of the spring diet came from caribou, which were also predated extensively (26-39%) by the Keily and Nevis packs. Also in winter 2003, members of the Dopp pack had moved to a new territory north of their former range and were renamed the Keily pack. Moose, in combination with elk, dominated the diets of the

Table 5.4. Estimates of mean seasonal prey composition (%) in the diets of wolves in the Besa Prophet study area using mean isotopic fractionation values (Table 5.3, from Roth and Hobson 2000). Seasons for which appropriate predator samples were not available were omitted. rbc indicates red blood cells.

			Signature		% Prey Composition							
Pack	**Season**	**Sample**	$\delta^{13}C$	$\delta^{15}N$	**Caribou**		**Moose**		**Elk**		**Sheep**	
					$\bar{X} \pm$ **SD**	**range**	$\bar{X} \pm$ **SD**	**range**	$\bar{X} \pm$ **SD**	**range**	$\bar{X} \pm$ **SD**	**range**
Dopp/Keily	Summer 02	whole hair	-22.01	5.23	3 ± 3	0-11	58 ± 7	44-75	31 ± 10	3-56	7 ± 5	0-22
	Fall 02	whole hair	-22.01	5.23	4 ± 3	0-12	75 ± 4	68-83	16 ± 4	6-29	6 ± 4	0-18
	Winter 03	Mar rbc	-23.47	5.14	18 ± 11	0-42	11 ± 4	0-20	38 ± 12	7-64	33 ± 20	0-76
	Spring 03	Mar plasma	-22.69	6.71	39 ± 7	24-56	1 ± 1	0-6	7 ± 6	0-26	52 ± 11	18-76
Richards/	Summer 01	tip hair	-21.40	5.38	26 ± 8	1-42	44 ± 6	28-60	14 ± 10	0-45	16 ± 11	0-50
Prophet	Fall 01	root hair	-21.97	5.43	6 ± 4	0-18	61 ± 4	53-70	25 ± 5	11-39	9 ± 6	0-27
	Winter 02	Mar rbc	-23.47	5.64	10 ± 8	0-32	2 ± 2	0-8	42 ± 10	19-69	46 ± 16	0-76
	Spring 02	Mar plasma	-23.29	6.92	14 ± 10	0-43	3 ± 2	0-10	24 ± 12	0-58	59 ± 19	0-95
	Summer 02	whole hair	-21.79	5.27	4 ± 3	0-12	54 ± 7	39-72	34 ± 10	4-61	8 ± 6	0-24
	Fall 02	whole hair	-21.79	5.27	4 ± 3	0-14	72 ± 4	64-81	17 ± 5	6-31	7 ± 5	0-21
	Spring 03	Mar plasma	-22.91	6.60	48 ± 9	26-70	3 ± 2	0-10	12 ± 9	0-35	38 ± 16	0-69
Nevis	Summer 02	whole hair	-22.10	5.04	1 ± 1	0-4	67 ± 7	54-79	30 ± 7	13-46	3 ± 2	0-8
	Fall 02	root hair	-22.10	5.24	6 ± 4	0-19	79 ± 4	71-89	7 ± 4	0-19	8 ± 6	0-29
	Winter 03	Mar rbc	-23.56	5.04	16 ± 10	0-37	16 ± 4	7-25	40 ± 11	12-62	28 ± 17	0-66
	Spring 03	Mar plasma	-23.30	6.55	26 ± 13	0-52	14 ± 4	3-25	22 ± 13	0-51	38 ± 22	0-83
Pocketknife	Summer 01	tip hairs	-22.41	5.44	3 ± 3	0-10	34 ± 7	20-51	56 ± 9	29-80	6 ± 5	0-20
	Fall 01	root hair	-22.13	5.64	3 ± 2	0-9	49 ± 4	42-57	45 ± 4	35-55	4 ± 3	0-14
	Winter 02	Mar rbc	-24.14	6.29	3 ± 2	0-8	7 ± 3	2-13	85 ± 4	75-94	5 ± 4	0-15
	Spring 02	Mar plasma	-23.83	7.22	5 ± 4	0-17	2 ± 1	0-5	77 ± 7	60-90	16 ± 9	0-37
	Summer 02*	Whole hairs	-22.69	5.40	1 ± 1	0-4	39 ± 18	0-68	57 ± 19	23-100	3 ± 2	0-9
	Fall 02**	Whole hairs	-22.69	5.40	2 ± 2	0-6	58 ± 7	48-82	38 ± 6	18-50	3 ± 2	0-10
	Winter 03	Mar rbc	-24.12	5.82	3 ± 2	0-9	3 ± 2	0-7	89 ± 4	78-100	6 ± 4	0-17
	Spring 03	Mar plasma	-23.88	7.47	4 ± 3	0-12	1 ± 1	0-4	82 ± 6	66-93	13 ± 8	0-32

Table 5.4. Continued

Pack	Season	Sample	Signature		% Prey Composition							
			$\delta^{13}C$	$\delta^{15}N$	Caribou		Moose		Elk		Sheep	
					$\bar{X} \pm SD$	range	$\bar{X} \pm SD$	range	$\bar{X} \pm SD$	range	$\bar{X} \pm SD$	range
Lower Besa	Summer 01	whole hair	-22.11	5.87	5 ± 4	0-17	11 ± 7	0-30	72 ± 11	37-99	12 ± 8	0-33
	Fall 01	Dec rbc	-24.03	6.28	3 ± 3	0-10	3 ± 2	0-9	89 ± 4	80-100	5 ± 4	0-16
	Winter 02	Mar rbc	-24.05	5.89	2 ± 1	0-7	8 ± 2	2-13	86 ± 4	76-94	5 ± 4	0-13
	Spring 02	Mar plasma	-23.77	7.53	8 ± 6	0-24	3 ± 2	0-8	70 ± 7	50-87	20 ± 11	0-44
	Summer 02*	whole hair	-22.68	5.37	1 ± 1	0-5	46 ± 19	5-77	50 ± 20	12-95	3 ± 3	0-11
	Fall 02**	whole hair	-22.68	5.37	2 ± 2	0-7	61 ± 8	50-84	35 ± 6	16-48	3 ± 2	0-11
	Winter 03	Mar rbc	-23.80	5.75	7 ± 5	0-22	2 ± 2	0-8	73 ± 7	55-89	18 ± 10	0-40
	Spring 03	Mar plasma	-23.64	6.89	13 ± 8	0-32	8 ± 3	0-16	55 ± 9	29-75	24 ± 15	0-58

* tolerance = 0.3‰

** tolerance = 0.25‰

Tolerance varied in order to provide feasible solution set; results are conservative relative to a tolerance of 0.1‰ in most model runs.

western and central packs in summer and fall, as determined from the mean estimates of prey consumption. The Pocketknife pack in the southeast and the Lower Besa pack in the northeast showed a much more consistent reliance on elk throughout the year (Table 5.4).

Even the small range in feasible fractionation values of N (0.4‰ – 1.0‰) and C (0.6‰ – 1.6‰) (Table 5.3) resulted in sizeable shifts in the estimates of mean prey proportions in the diets of wolves (Table 5.5), and in some cases resulted in different prey items being estimated as the dominant (>50%) prey. For example, in 31 of 36 solution sets, either moose (11-64%) or elk (8-64%) was estimated, on average, to be the dominant prey item in the diets of the Keily and Nevis packs during winter 2003. Moose was the dominant prey item in 19 sets, and elk dominated 12 sets. Similarly, either caribou (15-64%) or sheep (21-75%) was estimated to be the dominant prey item in 10 of 16 solution sets in the diet of the Keily and Prophet packs during spring 2003. Caribou was the dominant item in 6 sets, and sheep dominated 4 sets, with the other 6 sets combining sheep and caribou to comprise >70% of the diet.

Summer dietary analysis of scat samples from wolves showed high variability among packs and between years within packs (Table 5.6). During summer 2002, moose (28%), elk (29%), and caribou (28%) contributed almost equally to wolf diets. During summer 2003, however, moose (55%) was the primary prey item found in scat samples, followed by elk (22%), caribou (14%), and sheep (4%). Across packs and years, scat samples contained a large proportion of juvenile animals (39-73%). The scat samples also contained a wider range of relatively uncommon prey items than used in the isotope models. Alternative prey items included squirrels, hares, voles, and birds which collectively were found in <5% of all scat samples. Beaver was found in 11% of the scats from the Nevis

Table 5.5. Ranges in the estimates of mean seasonal prey composition in the diets of wolves in the Besa Prophet study area based on a feasible range in fractionation values (see Table 5.3). Mean prey composition determined from mean fractionation values is shown in Table 5.4. *n* indicates the number of fractionation combinations that satisfied the 0.1‰ tolerance used in the IsoSource model. x indicates that a range was unavailable because *n* =1.

			% Prey Composition			
Pack	**Season**	**N**	**Caribou**	**Moose**	**Elk**	**Sheep**
Dopp/Keily	Summer 02	8	3 – 28	35 – 79	5 – 55	6 – 19
	Fall 02	8	3 – 24	54 – 88	2 – 27	4 – 17
	Winter 03	18	7 – 27	11 – 59	9 – 63	12 – 33
	Spring 03	9	15 – 64	1 – 15	6 – 26	29 – 75
Richards/Prophet	Summer 01	7	20 – 75	15 – 59	5 – 26	5 – 27
	Fall 01	8	5 – 28	40 – 74	4 – 35	7 – 27
	Winter 02	16	5 – 20	1 – 39	20 – 80	12 – 34
	Spring 02	7	5 – 28	1 – 10	14 – 35	38 – 71
	Summer 02	10	4 – 45	31 – 75	6 – 58	4 – 21
	Fall 02	9	3 – 45	46 – 85	2 – 28	5 – 19
	Spring 03	7	27 – 64	1 – 10	8 – 16	21 – 62
Nevis	Summer 02	7	1 – 22	48 – 87	5 – 33	3 – 17
	Fall 02	5	2 – 17	55 – 79	7 – 33	4 – 20
	Winter 03	18	4 – 22	16 – 64	8 – 64	8 – 28
	Spring 03	9	20 – 36	5 – 24	17 – 34	29 – 48
Pocketknife	Summer 01	3	3 – 4	12 – 57	33 – 80	6 – 7
	Fall 01	8	3 – 17	28 – 60	9 – 56	4 – 26
	Winter 02	2	2 – 3	7 – 15	77 – 85	49 – 50
	Spring 02	6	4 – 10	1 – 9	65 – 84	10 – 26
	Summer 02	1	x	x	x	x
	Fall 02	1	x	x	x	x
	Winter 03	5	2 – 3	3 – 34	58 – 89	5 – 6
	Spring 03	2	3 – 4	1 – 2	82 – 88	7 – 13
Lower Besa	Summer 01	3	5 – 12	5 – 17	45 – 72	12 – 38
	Fall 01	2	2 – 3	3 – 14	80 – 88	4 – 5
	Winter 02	4	2 – 3	8 – 31	62 – 86	4 – 5
	Spring 02	2	4 – 8	3 – 5	70 – 84	8 – 20
	Summer 02	1	x	x	x	x
	Fall 02	1	x	x	x	x
	Winter 03	10	3 – 9	2 – 36	43 – 86	6 – 18
	Spring 03	9	3 – 13	2 – 23	47 – 85	5 – 30

Table 5.6. Percent occurrence of prey in scat samples (n = 345) from wolves during summer in the Besa-Prophet study area.

Pack	Year	N	% Occurrence of Prey										
			Moose		Elk		Caribou		Sheep		Goat	Beaver	Other[1]
			Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile			
Lower Besa	2002	17	17	11	22	22	6	6	0	0	0	0	17[2]
Lower Besa	2003	52	31[3]	31	4[4]	13	6	8	2[4]	2	0	0	4
Richards	2002	44	11	25	11	9	7	18	0	11	2	0	5
Prophet	2003	53	26	26	8	17	0	17	2	4	0	0	0
Nevis	2002	26	0	27	12[4]	19	8[4]	19	8	8	0	0	0
Nevis	2003	80	16	28	11	9	11	9	1	3	0	11	1
Dopp	2002	25	8	12	19	0	27	23	0	8	0	0	4
Keily	2003	48	18	47	20	4	0	4	0	4	0	0	2

[1] Other refers to unidentifiable ungulate samples, birds, and small mammals.
[2] includes 2 prey samples identified as either moose or elk
[3] assumes 2 individuals of unknown age were adults
[4] assumes 1 individual of unknown age was an adult

pack during the summer of 2003. Beaver isotopic signatures, however, were not significantly different from the ungulate prey species and I could not incorporate them separately into the summer isotope prey models developed for wolves.

Proportions of prey by species, as determined from summer scat samples from the Dopp/Keily, Richards/Prophet, Nevis, and Lower Besa packs (Table 5.6) were similar to the mean isotopic determinations from those packs (Table 5.4). The overall relative occurrence of prey was slightly higher in scat samples than estimates from isotope models (Fig. 5.2). Consistently within species, however, isotopic determinations were higher for elk proportions and lower for caribou proportions in wolf diets compared to fecal samples.

Grizzly Bears

The ^{15}N of grizzly bears in the BP study area increased significantly from summer to fall ($P < 0.025$), indicating more meat in the diet (Fig. 5.3). Males consumed more meat than females ($P < 0.025$). On average, meat comprised 19% of the diets of females in the spring and summer and almost 50% in the fall, whereas diets of males consisted of approximately 30% meat in the spring and summer and 65% in the fall (from Eqn. 2).

There was considerable individual variation in seasonal prey selection (Table 5.7) among females and males using average prey signatures (Table 5.2) and mean fractionation values generated from regressions in Hilderbrand et al. (1996) (Table 5.3). Of 22 female bears analyzed, 8 consistently had primarily herbivorous diets (estimated plant proportion, P_p: 64-100%) in the spring and summer, 6 showed peaks in their plant consumption during the summer (P_p: 67-100%), 5 showed peak plant proportions in the diet during spring (P_p: 71-100%) with a consistent reduction in plant consumption through fall (P_p: 31-69%), and 3

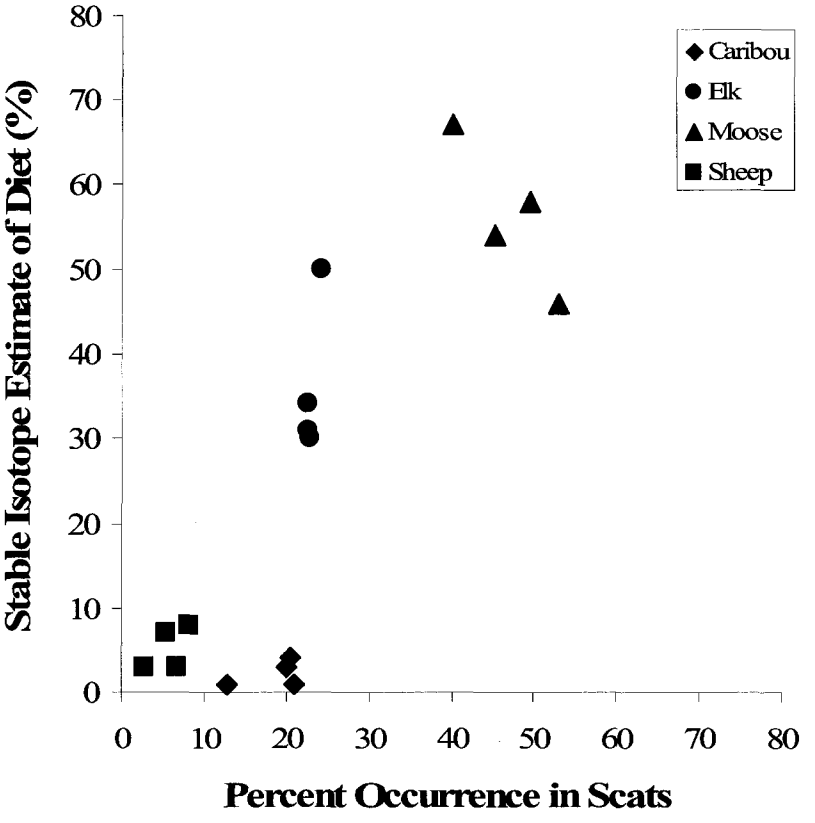

Figure 5.2. Comparison of dietary estimates for 4 packs (n =16) as determined by stable isotope and scat analyses for wolves in summer in the Besa-Prophet study area, 2002-2003.

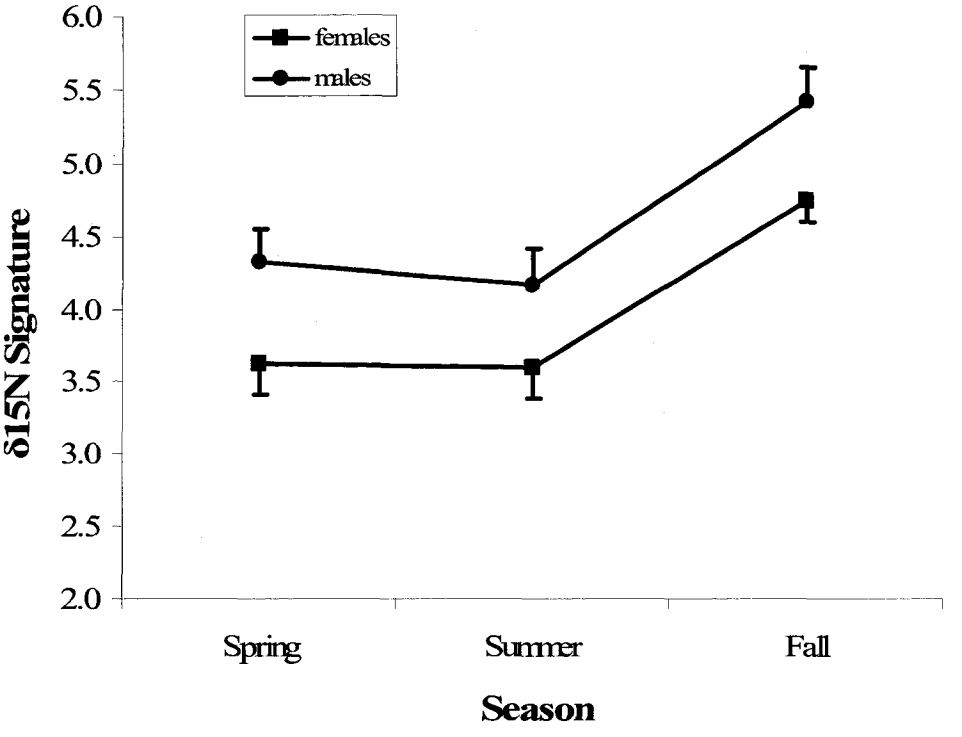

Figure 5.3. Seasonal variation in $\delta^{15}N$ signatures (mean ± SE) for male (n = 12) and female (n = 22) grizzly bears in the Besa-Prophet study area, as indexed by sectioned hairs.

increased their plant intake from spring (P_p: 48-55%) through fall (P_p: 61-70%). In 14 cases where the proportion of meat (P_a) in the fall diets of female grizzly bears was estimated to exceed 40%, elk was the largest ungulate prey source (estimated elk proportion, P_{elk}: 21-60%). Across seasons, moose (range: 0-18%), caribou (0-16%), and sheep (0-9%) each averaged less than 6% of the estimated meat proportion in the diet of female grizzly bears compared to 15% for elk (0-60%). Of 12 male bears analyzed, 3 had primarily herbivorous diets during the spring and summer (P_p: 56-100%), 5 showed peak plant intake during the summer (P_p: 60-100%), 3 showed a consistent reduction in plant consumption from spring (P_p: 71-77%) through fall (P_p: 0-31%), and only 1 male showed an increase in plant intake from spring to fall. Similar to females, the meat fraction in the diets of male grizzly bears across seasons was dominated by elk (21%, range: 0-60%), followed by moose (9%, range: 0-65%), sheep (7%, range: 0-13%), and caribou (5%, range: 0-14%). When compared to P_p determined using isotopic models that used the mean fractionation values (Table 5.3), Equation 2 yielded estimates across bears and seasons that were within the range predicted in 38 of 102 bear seasons, that were higher (1-13%) in 25 of 102 total bear seasons, and that were lower (1-13%) in 22 of 102 bear seasons. Models with the standard fractionation values of ΔN: 3.0‰ and ΔC: 2.0‰ used in many studies consistently had lower estimates of the proportion of plants (P_p: 0-47%) in the diets of male and female grizzly bears across seasons than estimates generated from either models using mean fractionation values for bears (Table 5.3), or derived from Equation 2.

Estimates in the mean proportions of ungulate prey in the diets of female and male grizzly bears were highly sensitive to the choice of fractionation values used in the models

(ΔN: 3.0 – 5.0‰; ΔC: 2.0 – 4.2‰) (Table 5.8). The average variation across individuals for the proportion of elk in all grizzly bear diets was 48 ± 14% for females (mean ± SD) and 52 ± 20% for males. Average variation was similar around the proportion of caribou (females: 30 ± 14%; males: 29 ± 13%) and moose (females: 26 ± 11%; males: 29 ± 15%), and lower for sheep (females: 15 ± 4%; males: 17 ± 5%). The maximum differences in estimated dietary proportions for individual female and male bears respectively were 84% (BN, fall) and 89% (I, fall) for elk, 69% (G18B, spring) and 63% (AG, fall) for moose, 55% (AN, fall) and 53% (AM, summer) for caribou, and 23% (G15B, fall) and 24% (I, fall) for sheep.

Discussion

Wolves

In this study I demonstrated seasonal variation in prey selection by wolf packs in the Besa-Prophet study area based on stable isotope analyses. Moose had been speculated to be the most important prey item for wolves throughout the year in northeastern British Columbia (Bergerud and Elliott 1986), but my results suggest that dietary dynamics of wolves are more complex than previously considered. Moose was a major prey item during summer and fall, particularly in the diets of the western packs, but elk (and in some cases sheep) were prey items in winter and spring (and even year round in the eastern packs). The prevalence of elk in the diets of wolves may be related to elk numbers tripling in the Peace-Liard region since the 1970's (Shackleton 1999). Elk have been observed to be consistently important in wolf diets in numerous other systems, including Yellowstone (Smith et al. 2004), Banff National Park (Hebblewhite et al. 2002), Glacier National Park (Kunkel et al.

Table 5.8. Variation in the mean estimates of prey composition in female (n = 22) and male (n = 12) grizzly bear diets generated when using a range of feasible fractionation values (ΔN: 3.0 – 5.0‰; ΔC: 2.0 – 4.2‰) constrained by regressions in Hilderbrand et al. (1996) and values typically cited in the literature. n indicates the number of fractionation combinations that satisfied the 0.1‰ tolerance used in the IsoSource model.

			% Prey Composition				
FEMALES	**Season**	***N***	**Moose**	**Elk**	**Caribou**	**Sheep**	**Grazers**
AB	Spring	4	6 - 41		6 - 21		5 - 42
	Summer						
	Fall	15	4 - 31	2 - 48	2 - 38	4 - 22	
AN	Spring						
	Summer						
	Fall	14	3 - 28	1 - 55	2 - 57	4 - 21	
AP	Spring						
	Summer						
	Fall	12	4 - 33	3 - 52	4 - 30	4 - 19	
AR	Spring						
	Summer						
	Fall	9	5 - 25	4 - 52	3 - 19	4 - 16	
AW	Spring	5	6 - 55		6 - 18		4 - 40
	Summer	10	5 - 27	4 - 67	4 - 40	5 - 22	
	Fall	14	5 - 32	1 - 61	3 - 44	4 - 23	
BC	Spring						
	Summer	9	3 - 19	2 - 38	2 - 16	2 - 11	
	Fall	11	4 - 21	2 - 43	2 - 28	3 - 18	
BN	Spring	5	5 - 21		5 - 16		6 - 23
	Summer	10	7 - 25	4 - 39	2 - 23	6 - 17	
	Fall	9	4 - 26	2 - 86	2 - 32	4 - 21	
BS	Spring	9	6 - 38		6 - 29		4 - 45
	Summer						
	Fall	16	6 - 31	2 - 67	3 - 44	6 - 24	
BY	Spring						
	Summer	12	7 - 28	3 - 53	2 - 54	6 - 18	
	Fall	13	5 - 33	5 - 58	3 - 26	4 - 21	
C	Spring	8	6 - 30		6 - 24		5 - 45
	Summer	6	4 - 18	4 - 41	3 - 13	4 - 11	
	Fall	12	4 - 31	4 - 53	3 - 25	4 - 21	
CG	Spring	6	9 - 28		9 - 26		8 - 43
	Summer	13	6 - 27	5 - 46	2 - 51	5 - 19	
	Fall	10	3 - 29	2 - 84	2 - 19	3 - 22	
CZ	Spring						
	Summer						
	Fall	10	5 - 20	1 - 37	3 - 46	4 - 17	

Table 5.8. Continued

			% Prey Composition				
FEMALES	**Season**	***N***	**Moose**	**Elk**	**Caribou**	**Sheep**	**Grazers**
L	Spring						
	Summer						
	Fall	12	3 - 26	1 - 38	2 - 43	3 - 21	
M	Spring	6	6 - 31		5 - 23		8 - 41
	Summer	7	6 - 23	2 - 17	3 - 37	3 - 18	
	Fall	11	4 - 29	1 - 58	4 - 32	4 - 19	
O	Spring						
	Summer						
	Fall	14	4 - 23	1 - 42	2 - 44	4 - 21	
G01B	Spring	8	6 - 48		5 - 21		3 - 28
	Summer	10	6 - 19	2 - 30	2 - 25	4 - 16	
	Fall	13	4 - 33	4 - 56	2 - 25	3 - 18	
G15B	Spring	11	6 - 46		5 - 36		4 - 42
	Summer	12	8 - 26	3 - 48	3 - 55	3 - 16	
	Fall	17	3 - 30	1 - 65	3 - 46	2 - 25	
G18B	Spring	11	12 - 81		12 - 37		3 - 52
	Summer	12	7 - 26	3 - 50	2 - 53	4 - 16	
	Fall	14	3 - 29	1 - 63	2 - 46	3 - 23	
G26A	Spring	11	6 - 63		6 - 27		3 - 55
	Summer	11	6 - 24	2 - 43	3 - 55	3 - 14	
	Fall	13	3 - 32	5 - 56	2 - 24	3 - 16	
G27A	Spring	9	12 - 41		12 - 35		6 - 51
	Summer	11	5 - 29	2 - 50	2 - 33	3 - 18	
	Fall	13	4 - 32	4 - 53	2 - 27	3 - 16	
G28A	Spring	5	7 - 26		6 - 21		10 - 48
	Summer	5	10 - 16	6 - 37	4 - 25	9 - 14	
	Fall	11	3 - 22	2 - 63	3 - 41	3 - 19	
GYF	Spring	13	6 - 56		5 - 32		4 - 70
	Summer	10	4 - 26	2 - 42	1 - 32	3 - 15	
	Fall	11	6 - 21	1 - 39	2 - 44	2 - 18	
MALES							
AG	Spring	11	5 - 61		5 - 26		3 - 56
	Summer	10	4 - 23	3 - 34	1 - 27	5 - 19	
	Fall	3	2 - 65	28 - 79	3 - 8	5 - 11	
AM	Spring	9	12 - 39		11 - 34		7 - 52
	Summer	11	5 - 27	2 - 42	3 - 56	3 - 15	
	Fall	15	3 - 28	1 - 67	2 - 51	2 - 25	
AO	Spring	11	6 - 62		6 - 27		4 - 59
	Summer	10	5 - 28	5 - 71	4 - 39	6 - 25	
	Fall	14	4 - 34	1 - 55	3 - 38	4 - 27	

Table 5.8. Continued

			% Prey Composition				
MALES	**Season**	**n**	**Moose**	**Elk**	**Caribou**	**Sheep**	**Grazers**
BQ	Spring	10	6 - 60		6 - 24		4 - 70
	Summer	9	9 - 25	4 - 26	4 - 34	6 - 23	
	Fall	13	3 - 30	1 - 78	2 - 40	3 - 21	
BX	Spring	9	5 - 35		6 - 28		5 - 37
	Summer	11	4 - 29	5 - 68	4 - 48	5 - 24	
	Fall	14	2 - 31	2 - 89	2 - 47	3 - 25	
BZ	Spring						
	Summer						
	Fall	15	3 - 28	1 - 64	2 - 49	2 - 25	
CU	Spring	5	5 - 18		5 - 17		6 - 50
	Summer						
	Fall	10	3 - 26	4 - 46	2 - 20	3 - 17	
I	Spring	8	5 - 30		5 - 27		3 - 43
	Summer	11	4 - 24	2 - 32	1 - 45	3 - 20	
	Fall	15	2 - 30	2 - 91	2 - 43	2 - 26	
Q	Spring	11	6 - 74		6 - 30		4 - 51
	Summer						
	Fall	13	5 - 32	6 - 59	3 - 27	5 - 22	
S	Spring	8	6 - 33		5 - 24		4 - 42
	Summer	7	5 - 24	5 - 63	2 - 36	5 - 17	
	Fall	1	x	x	x	x	x
GKM	Spring	1	x		x		x
	Summer	4	9 - 18	5 - 24	3 - 25	7 - 15	
	Fall	7	3 - 20	3 - 47	2 - 18	3 - 15	
GPM	Spring	8	9 - 34		9 - 29		4 - 41
	Summer	10	4 - 23	4 - 37	2 - 25	4 - 13	
	Fall	15	3 - 31	1 - 62	2 - 50	2 - 23	

2004), Jasper National Park (Dekker et al. 1995), and Riding Mountain National Park (Carbyn 1983).

Without accurate estimates of seasonal relative prey abundances in my area, I can only speculate that the observed differences in prey use by wolves in the BP are in response to seasonal shifts in local prey composition and relative densities within the home ranges of each individual pack. In Europe, studies have concluded that the breadth of the food niche of wolves is directly related to the number of ungulate species in the community (Okarma 1995), the spatial distribution of prey availability (Mattioli et al. 1995; Meriggi et al. 1996), shifts in densities of preferred prey (Jedrzejewski et al. 2000) as well as the availability of locally abundant alternative non-ungulate prey (Gade-Jorgensen and Stagegaard 2000). Similar patterns have been observed in North America. Wolves have been shown to switch to alternate prey in response to the migratory patterns of primary prey populations (Ballard et al. 1997) or to changes in densities of non-migratory primary prey (Forbes and Theberge 1996). Seasonal and spatial variation in prey use by wolves was related to the location of the home range in Yellowstone National Park (Smith et al. 2004). The presence of alternative non-ungulate prey in the diets of Alaskan wolves depended on differences in habitat (e.g., logging treatments) (Kohira and Rexstad 1997). It has been suggested that when selecting a home range, wolf packs may be making a trade-off between the encounter rate and the profitability of available prey within the area (Kunkel et al. 2004).

The adaptability of wolves is clearly highlighted by regional differences in prey composition related to the local composition and relative abundance of the available prey base. Several authors report a difference in diet between packs occupying neighbouring

territories (Gade-Jorgensen and Stagegaard 2000). Diet specialization of individual wolf packs also may be related to wolf pack size, pack-specific feeding habits, environmental conditions within territories, and hunting pressure on wolves (Okarma 1995; Spaulding et al. 1998; Gade-Jorgensen and Stagegaard 2000). The majority of studies addressing diet selection by wolves have focused on the summer and winter seasons, and have been based on scat analyses and backtracking to kill sites. Other studies have utilized stable-isotope techniques to estimate seasonal variation in canid diets (Darimont and Reimchen 2002; Roth 2002). My study demonstrated the potential use of stable isotopes in obtaining a finer resolution in dietary analyses that is dependent on the selection of multiple sample types (hair, blood, meat) for analysis.

The analyses of scat samples indicated that, as observed in other studies (Mattioli et al. 1995; Husseman et al. 2003; Smith et al. 2003), juveniles comprised a significant portion of the diets of wolves in summer. The advantages of scat analyses over isotopic estimates are in potential age determination of prey items and the identification of relatively uncommon prey items. Disadvantages, however, include a bias against highly digestible prey material, and dietary estimates are only for the population level. Furthermore, scat samples in my study were pooled from two years of collections, and assumed to represent average summer diets of wolves. Scat analyses are also a relatively short-term dietary assessment that indexes recent ingestion compared to the longer-term estimates from stable isotopes that index not only what was eaten, but the assimilation of prey material into consumer tissues utilized for growth and maintenance. The similarity between the scat analysis and stable isotope analysis lent support to the use of fractionation values determined from captive foxes (Roth and Hobson 2000). Stable-isotope dietary estimates

for wolves in the boreal forest of Saskatchewan that utilized similar fractionation values were also consistent with statistically corrected percent biomass consumption estimates based on faecal analyses (Urton and Hobson 2005). Furthermore, dietary patterns by wolves in the BP as revealed by stable isotope analyses are also in agreement with patterns of selection for vegetation classes (e.g., shrub, burn categories) that may increase their likelihood of encountering moose and elk (Chapter 3).

Grizzly Bears

My results were consistent with the prediction that male grizzly bears were more carnivorous than females, but at the population level for both sexes, carnivory was higher during the fall than spring. There was, however, considerable individual variation in meat consumption. The use of ungulates by grizzly bears has been widely demonstrated (Servheen 1983; Reynolds and Garner 1987; Boertje et al. 1988; Larsen et al. 1989; Ballard et al. 1991; Schwarz and Franzmann 1991; Gasaway et al. 1992; Green et al. 1997; Mattson 1997; Young and McCabe 1997). I was able to demonstrate seasonal variation in ungulate resources in the diets of grizzly bears based on the assumption that hair from bears in good condition has a constant growth rate from the onset of molt in spring until the fall (C.T. Robbins, pers. comm.; Jacoby et al. 1999). Metabolically inert tissue, such as hair, retains dietary information in a chronological order during the period of growth (Hobson and Clark 1992b; Darimont and Reimchen 2002). Whiskers from captive harp seals (*Pagophilus groenlandicus*) fed a constant diet, for example, showed negligible variation in $\delta^{15}N$ and $\delta^{13}C$ when sectioned at 5-mm intervals (Hobson et al. 1996). Variation in isotopic signature along the length of the whisker would be evidence of dietary change.

Jones et al. (2006) cautioned against using sectioned guard hairs in diet inferences. They based their assertion on comparisons of stable isotope signatures between underfur, assumed to grow in the fall, and sectioned guard hairs, assumed to grow throughout the year. There was variable overlap between underfur signatures and guard hair sections corresponding to fall. If all guard hair grows at a constant rate and stops growing at the same time in autumn, then variation in isotope values within guard-hair sections of a fixed length should vary within analytical error (Jones et al. 2006). The degree of variation in $\delta^{15}N$ signatures exceeded that explained by analytical error in their study, and they concluded that their assumptions regarding hair growth may have been false. Assumptions on constant growth rates of guard hairs, as well as onset and cessation of hair growth, are premised on the body condition of grizzly bears (Jacoby et al. 1999). Grizzly bears from the Parsnip region of central British Columbia are in reasonably good condition (Ciarniello 2006). The underlying assumption to the analysis conducted by Jones et al. (2006) is that irrespective of the onset of growth, and independent of body condition, the root section of the hair will always be grown in late summer or fall, as will the underfur. It is unclear, however, what type of information is lost by sectioning hairs at arbitrary 30-mm intervals and discarding the distal end (as in Jones et al. 2006), and the conclusions that can be derived from this process. The analysis of whole guard hairs represents an average isotopic signature during the period of growth, and masks seasonal variability and the importance of different food types during the year (e.g., Mizukami et al. 2005 a,b). Similarly, by sectioning guard hairs into arbitrary sections and discarding portions of the hair, one is potentially masking seasonal effects by unintentionally overlapping, and subsequently averaging, periods of dietary shifts. By discarding a portion of the hair, the ability to

calibrate the time frame is lost, and it is uncertain whether 30-mm sections of hairs compared across bears with different hair lengths are representing the same thing. A portion of this uncertainty is removed by sectioning hairs in equal proportions. I used equal proportions for hairs from bears in the BP. No information is lost, and it removes errors associated with individual variability in hair lengths. Errors associated with seasonal overlap are still possible, but reduced. Irrespective of the onset of growth (based on body condition), sections provide a dietary index for a specific time period (assuming a constant rate once hair growth is initiated and that we know when it starts and ends).

For example, the sectioning of guard hairs has been used to track fine-scale variation in the dietary composition of Asiatic black bears (*Ursus thibetanus*) (Mizukami et al. 2005a,b). In this population, hair begins to grow in May after hibernation and stops growing before hibernation. Hair was sectioned every 3 mm or 5 mm to identify seasonal differences in foraging patterns amongst and between alpine bears removed from human influence and nuisance bears with access to anthropogenic food sources. Distinct patterns were identified along the length of guard hairs that were related to dietary change throughout the year (after Hobson et al. 1996) and that would have been masked had analyses solely focused on whole hairs.

The increase in meat consumption by both male and female grizzly bears in the BP during the fall appears to be primarily elk. This is not unreasonable given that bears and elk may overlap in habitat selection for the high vegetation biomass in prescribed burn areas. Stable isotopes cannot distinguish signatures from scavenged meat and prey that was depredated. Changes in the distribution of bears in response to ungulate harvests have been observed in Yellowstone National Park (Haroldson et al. 2004). The prevalence of elk in

the fall diet of bears in the BP may suggest some level of predation, but the contribution of both spring and fall carrion (e.g., gut piles) versus predation needs further study. Nutritional ecology studies suggest that bears that eat meat in the spring tend to add lean body mass, whereas in fall excess protein is converted to fat (Hilderbrand et al. 1999b; Mowat and Heard 2006).

Other studies have used stable isotope analyses to examine the diets of wild, captive, and extinct bears (Hilderbrand et al. 1996; Hilderbrand et al. 1999b; Hobson et al. 2000; Felicetti et al. 2003a; Bocherens et al. 2004), but most have not examined species-specific estimates of general meat and plant consumption. Hilderbrand et al. (1999a) used blood signatures from repeated captures of brown bears to examine seasonal meat intake related to body mass and composition, and concluded that meat, and particularly salmon intake, influences population density at the continental scale. Meat intake may influence population densities at finer scales as well (Mowat and Heard 2006).

I examined seasonal prey selection by bears in a complex prey community by analyzing seasonal bear signatures with seasonal prey signatures. My results are consistent with the conclusion that in non salmon-bearing systems, males are significantly more carnivorous than females (Hilderbrand et al. 1998; Jacoby et al. 1999). Maximum mass gain by bears consuming herbaceous vegetation is constrained by the ability to digest vegetation (Rode et al. 2001). Meat intake is significantly correlated with mean adult female body mass, mean litter size, and mean population density (Hilderbrand et al. 1999b). The mean $\delta^{15}N$ (3.80‰) and $\delta^{13}C$ (-22.65‰) hair signatures for female grizzly bears in the BP are similar to those reported from other non-salmon systems (in Hiderbrand et al. 1999b). Average annual meat consumption by female grizzly bears, as reflected by isotopic

assimilation into hair, was 26% in the BP. Using this mean consumption in relationships derived by Hilderbrand et al. (1999b), females in the BP are predicted to weigh ~148 kg with a range of 113-172 kg (female grizzly bears in the BP are estimated at 100 – 150 kg in early spring, R. Woods, pers. comm.), have a mean litter size of 2.1 (mean of 2.0 observed in the BP), and support a mean density of <50 bears/1,000 km^2 (densities of 35 bears/1,000km^2 were reported in the foothills and western portions of my study area; Poole et al. 2000). The availability of meat is an important resource for grizzly bear populations (Hilderbrand et al. 1999a,b) and terrestrial meat may provide the majority of assimilated resources in body proteins in some ecosystems (Mowat and Heard 2006). In the BP, however, plants provided the majority of nutrients assimilated into both male and female grizzly bears. The relative amounts of different plant species consumed could not be determined by stable isotope analyses.

Importance of Seasonal Signatures and Fractionation Values

Since the seminal papers of DeNiro and Epstein (1978, 1981), there has been considerable interest in using stable isotopes in ecological research. Over the last 15 years there has been a marked increase in the use of stable isotope techniques to elucidate food-web dynamics and energy flow across a wide variety of taxa and systems (Post 2002). There can be considerable uncertainty and variability in the estimation of prey proportions in consumer diets based on mixing models developed for stable isotope data, and the limitations and assumptions in these techniques have been discussed at length (Ben-David and Schell 2001; Phillips 2001; Phillips and Gregg 2001, 2003; Koch and Phillips 2002; Phillips and Koch 2002; Robbins et al. 2002, 2005). One source of uncertainty is establishing appropriate baseline prey signatures (Post 2002), and I have attempted to

accommodate this variation by incorporating baseline signatures analyzed from prey in the BP, and using isotopic signatures from tissues appropriate for the season being examined.

One of the assumptions using isotopic models is that prey isotopic signatures are significantly different. Phillips and Greg (2003) reported that differences between mean prey isotopic signatures ideally should be larger than 2‰, but differences of 1‰ with a SD of less than 0.3 could provide prey proportion estimates with 95% confidence that the mean is ±10% of the estimated value. The latter case applies to my study. Smaller differences between isotopic prey signatures result in even greater variation in the estimates of prey proportions in consumer diets because each prey item has a proportionately greater likelihood of contributing to the consumer diet.

The application of mixing models to dietary reconstructions is limited by the estimation of appropriate fractionation values (Phillips and Koch 2002). Fractionation may vary with food type, among consumer species, among tissues and organs within an organism, and with physiological stressors (Venderklift and Ponsard 2003). Conclusions from previous dietary analyses typically have been based on a single fractionation value derived from an identical or taxonomically related consumer species, or on the unweighted mean and variance of fractionation values of unrelated organisms (Venderklift and Ponsard 2003). Using fractionation values from unrelated taxa may be inappropriate. My analysis demonstrates how the choice of a fractionation value can influence inferences in diet reconstructions. I was able to apply fractionation values generated from captive bears and captive foxes to my study. Although differences in metabolic rates and physiological condition may differ between captive and wild animals (Hobson and Clark 1992b), my data

suggest that this process may be more robust than the use of an unweighted mean that is generally applied across taxa (Post 2002).

Two conflicting hypotheses link nitrogen fractionation to protein quantity (Pearson et al. 2003; nitrogen fractionation would increase with nitrogen concentration, and therefore, across trophic levels) or quality (Roth and Hobson 2000; nitrogen fractionation would decrease with increasing protein quality or trophic level). Ultimately both protein quantity and quality may be important in understanding fractionation within and across trophic levels (Robbins et al. 2005). The issue may be more complex than previously considered. In their assessment linking nitrogen fractionation to dietary nitrogen content and C:N ratios, Robbins et al. (2005) reported mean nitrogen fractionation values of 4.0 ± 0.2‰ (n = 3) in blood components of mammals feeding on mammals. They assumed there were no differences between the blood constituents when equilibrated with the diet (e.g., Hilderbrand et al. 1996; but see also Roth and Hobson 2000). They recommended using these values in studies of carnivores if study-specific values cannot be generated. Their mean is similar to my value (mean = 4.2) for plasma, but different from the value used for red blood cells (mean = 2.6) in my analyses of wolf diets (Table 5.3). For omnivorous animals, or animals with complex diets, one cannot assume that a fractionation value can be predicted from the weighted average of all dietary components (Robbins et al. 2005). For grizzly bears, they reported fractionation values in plasma that range from 1.8‰ in bears on a milk diet to 5.8‰ for bears on a frugivorous diet. Assuming no difference in fractionation between blood components and hair, the fractionation values I used in my dietary assessment for grizzly bears in the BP (Table 5.3) fall within this range.

My results indicate that even small changes in fractionation inputs can result in wide shifts in the estimates of prey contribution to consumer diets. As another example, dire wolves (*Canis dirus*) from the late Pleistocene consumed a large proportion of bison, camel, and other dire wolves based on non-specific trophic fractionations of 1‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$ (Deniro and Epstein 1978) (Fox-Dobbs et al. 2007). When based on carnivore-specific fractionation values for bone collagen of 1.3‰ and 4.6‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively, however, dire wolves consumed primarily horse with equal but lower contributions of sloth, mastodon, and grazers (camel and bison) (Fox-Dobbs et al. 2007). It is important that results from mixing models be taken as indices of relative prey composition rather than absolute measures (Ben-David and Schell 2001; Phillips 2001; Robbins et al. 2005). Stable-isotope analysis can be a valuable tool to ecologists, but until a more detailed understanding of the underlying mechanisms of diet-tissue fractionation is developed, diet reconstructions using stable isotope techniques should base conclusions on a constrained and feasible range of fractionation values, particularly in studies where fractionation values from identical or related taxa are unavailable. Studies using stable isotope techniques in diet reconstructions should report the fractionation values that were used in the models, as well as the source of those values, to allow for comparisons across studies. Results from stable isotope analyses can further be strengthened or verified in conjunction with concurrent habitat selection studies.

Predator-Prey Relationships in the Besa-Prophet Ecosystem

The BP in northeastern BC has an intact suite of large-mammal predators and prey, and offers the opportunity to study ecosystem-level patterns in a relatively non human-impacted system. I used stable isotopes of carbon and nitrogen to identify predator-prey

relationships for 2 of the dominant predators in this system, wolves and grizzly bears, and their ungulate prey. The overlap in habitat use by these predators (see Chapters 3 and 4) and utilization of the same prey base may have significant implications for conservation and management of this system. In broad-scale ecosystem level studies, Husseman et al. (2003) and Kunkel and Pletscher (1999) demonstrated a dynamic link between fluctuations in ungulate populations and the differential habitat use and prey selection by multi-predator communities in Idaho and Glacier National Park, respectively. Similarly in the BP, predation by wolves and grizzly bears could be a limiting factor for increases in elk populations.

The majority of research in North America has emphasized the dominant role of wolves in predator-prey dynamics (Carbyn et al. 1995). Although the importance of ungulates in grizzly bear diets has been established (Mattson 1997; Young and McCabe 1997), the relative and cumulative impacts of wolves and grizzly bears on ungulate population dynamics is still unclear. The consumption of ungulate material by bears warrants further investigation into the potential contribution of grizzly bears towards structuring ungulate communities in the BP. Further evaluation is needed to determine how strategies of predators impact prey populations differentially, and how prey selection patterns cumulatively impact the population demography and behavioural responses of prey (Husseman et al. 2003). Stable-isotope techniques, when combined with detailed GPS location data and habitat selection information from both predators and their prey, may help identify seasonal variation in functional responses in complex multi-predator multi-prey systems.

Chapter 6: Predator Dynamics on the Besa-Prophet Landscape

Introduction

Wolves and grizzly bears are the dominant large mammal predators on the Besa-Prophet landscape, and are probably in sufficient numbers to regulate the abundance and distribution of an extensive ungulate community. Large mammal predator-prey research in British Columbia has tended to focus on two scenarios. First is that of a single predator regulating a single prey population (e.g., wolves and moose: Bergerud et al. 1983; wolves and caribou (*Rangifer tarandus*): Bergerud and Elliott 1986). Second is the capacity of a single predator to regulate a multi-prey community (e.g., Bergerud and Elliott 1998). In the Muskwa-Kechika Management Area, moose are thought to be selected preferentially by wolves, yet caribou continue to be maintained at low densities (R. Woods, British Columbia Ministry of Environment, pers. comm.). The majority of research in North America has emphasized the dominant role of wolves in predator-prey dynamics (Carbyn et al. 1995). Although the importance of ungulates in grizzly bear diets has been established (Mattson 1997; Young and McCabe 1997), the relative and cumulative impacts of wolves and grizzly bears on ungulate population dynamics is still unclear.

Grizzly bears will typically eat meat whenever it is available. They can be effective terrestrial scavengers and predators (Mattson 1997). Predation by both black and grizzly bears on ungulate calves can potentially regulate ungulate populations at low densities (Reynolds and Garner 1987; Boertje et al. 1988; Larsen et al. 1989; Ballard et al. 1991; Schwarz and Franzmann 1991; Gasaway et al. 1992). How the use of ungulates and rates of predation vary with shifts in ungulate species composition, the availability of alternate

resources (e.g., vegetation), and spatial and temporal variation in ungulate distributions and densities remains unclear.

My data show that moose and elk are significant prey in the diets of wolves, but that caribou, and to a lesser extent Stone's sheep, may be seasonally important to some packs. Both male and female grizzly bears consume more meat in the fall, and elk are their primary meat source (whether elk are scavenged from hunter kills or predated is unknown although 2 observations (B. Milakovic, unpub. data) of female grizzly bears pursuing elk suggest some level of predation). GPS data provide information about where animals are and the amount of space they use. This information can be used to generate RSFs that reflect the relative value of habitat classes within that space over time. How animals use space over time, and the degree to which animals share that space, ultimately drive patterns of population distribution and interaction. Although stable isotopes provide only an index of prey consumption, they nevertheless serve as an assessment of the strength of predator-prey interactions. From a management perspective, it is informative to know that wolves are eating primarily moose or elk. Changes to the landscape that alter the distribution of these ungulates may have significant impacts on alternative prey. Prey switching by predators provides insight into local prey movements associated with changes in local vegetation and to times when certain prey may become more vulnerable (e.g, calving, rut). Such information can be obtained over a relatively shorter time frame than field data on functional and numerical responses, is valuable to managers, and is based on how animals are using the landscape versus computer simulations of population responses.

My approach extends beyond expert-based approaches such as Habitat Suitability Indices (HSI) that are of a coarser grain (polygons with numerous vegetative and

topographical features), are species-specific, and are developed for a single season (e.g., spring for grizzly bears, or winter for ungulates) because it identifies the relative value of habitat classes and landscape features (GPS/RSF) and examines linkages (stable isotopes) in the system. Rather than the conservation of only a single species, management decisions should be based on tools that enable us to better understand ecosystem function. In areas open for development, the goal should be to enable access to the resource while conserving both ecosystem function and the potential of the landscape to support diverse wildlife (e.g., the large-mammal predatory-prey system).

In my study, I determined ranges and movements, habitat use and selection, and food habits of wolves and grizzly bears as part of a collaborative endeavour to characterize the ecosystem-level dynamics of a relatively intact large-mammal system. I summarize these findings in this chapter, and present them in the context of provincial habitat models currently being used to manage the landscape. Some of this material is in addition to the previous chapters; it is presented in relation to the provincial habitat models for the benefit of land-use plans in the Besa-Prophet.

Movements and Ranges

Wolves and grizzly bears used most areas of the Besa-Prophet study area. Movement rates were generally higher and range sizes tended to be larger for wolves than for female bears. Movement rates (determined from 6-hr GPS fixes) of wolves in the BP averaged 3.2 km/6hr, tending to peak during the denning period (3.6 km/6hr) and to be lowest during the winter months (2.4 km/6hr). Seasonal movement rates of individual female grizzly bears in the BP did not exceed 2.7 km/6hr, averaging approximately 1.2 km/6hr. I was unable to compare movement rates of males and female bears, but females

with cubs-of-the-year (COY) had significantly lower movement rates during spring and summer than other family groups. These movement patterns may be related to avoidance of conspecifics or limited mobility of young.

Annual home ranges of wolf packs in the BP were between 375 and 1333 km^2, and depended on relative habitat productivity, adjusted for pack size (area available per wolf). Other studies also have shown a weak to moderate positive relationship between pack size and territory/range size (Fuller et al. 2003). Annual range sizes reported for wolves vary between 200 km^2 and >2000 km^2 (Cook et al. 1999; Walton et al. 2001), depending on density and availability of preferred and alternative prey. Most studies that have concentrated on territorial wolves that prey on ungulates, including deer, elk, moose, and sheep, have concluded that wolves maintain relatively stable annual territories (Walton et al. 2001). Ungulate diversity and abundance may facilitate stable habitat occupancy by wolves (Massolo and Meriggi 1998) because multi-prey assemblages can limit large fluctuations in prey supply and predator densities. There was, however, considerable variation in sizes of seasonal ranges of wolves in the BP. Sizes of winter and late winter ranges appeared to be a function of movement rates, whereas sizes of denning and late summer ranges were proportional to the extent of conifer habitats. Differences between summer and winter ranges and habitat use may be related to den use and pup rearing (Cook et al. 1999; Walton et al. 2001).

Among grizzly bears, movement rates and range sizes are typically greater for males than females, and differ between adults and subadults, and between lone adult females and females with young (Servheen 1983; Blanchard and Knight 1991; Mace and Waller 1997). Average annual home ranges of female grizzly bears in the BP ranged from 82 to 582 km^2

based on 95% MCPs. These sizes spanned the reported values in other northern mountain grizzly bear populations of western Canada: 252 km^2 for females with cubs in West Central Alberta (WCA); and 210 km^2 in northern Yukon, 393 km^2 in Jasper National Park (JNP), and 476 km^2 in WCA for females without cubs (Nagy and Haroldson 1990). Average annual MCPs for adult males were 645 km^2 in Yukon, 948 km^2 in JNP, and 1,918 km^2 in WCA. Sizes of the annual home ranges of female grizzly bears in the BP were inversely related to the extent of available *Elymus*-dominated burns and disturbed habitat (including avalanche chutes), which is consistent with other observations that home ranges of grizzly bears are inversely related to overall habitat productivity (McLoughlin and Ferguson 2000). Home ranges of COY family units were significantly smaller during spring than those of other family units. Prescribed burning and other disturbance types may provide additional benefits in terms of range selection by grizzly bears. The degree to which this enables home range overlap and high population densities of grizzly bears merits further investigation.

Habitat Use and Selection

In the Besa-Prophet, which is relatively non-impacted by human activity, wolves appeared to show fine-grain spatial patterns by specifically responding to habitats within their home ranges. Generally, wolves avoided conifer habitat relative to availability, but considering the high level of overall use, forest cover may still be used by wolves for security cover during denning and rendezvous periods. Shrub areas and complex habitats (with high fragmentation) were selected year round by wolves, and regenerating disturbed habitats were also seasonally selected. It seems likely that at higher orders of selection, wolf occupancy is first dependant on prey density. Subsequent spacing of ranges on the landscapes may depend on intra-specific competition and to some extent pack size. To

maximize fitness and pack survival, day to day habitat use is probably a function of territory boundary defense, hunting efficiency, and minimizing energy expenditure, all of which operate within an annual cycle of pup rearing (Kreeger 2003; Packard 2003). These factors are directly influenced by habitat and other landscape features to which wolves respond.

Female grizzly bears in the BP were generally found at higher elevations during spring and lower elevations during fall. They tended to be more distributed across elevational gradients during summer. During spring and fall, female grizzly bears typically used south and east aspects, and in summer increased their use of north aspects. Shrub and burn habitat classes were generally selected year-round, whereas conifer classes were consistently avoided. Habitat selection by grizzly bears was best predicted from habitat class, elevation, aspect, and vegetation diversity. As with grizzly bears in the Flathead River drainage of southeastern BC (McLellan and Hovey 2001), grizzly bears in the BP are free to choose between high and low-elevation habitats. Most reported elevational movements are in response to variations in plant phenology (Stelmock and Dean 1988; Darling 1989; Hamer and Herrero 1990; Ciarniello 2006). Prescribed burning in the BP for the management of elk and Stone's sheep may provide specific foraging opportunities for bears. Management options should maintain a diverse habitat matrix distributed across a large elevational gradient for grizzly bears.

Resource Selection Surfaces

To visualize relative selection of the Besa-Prophet landscape to wolves and female grizzly bears, I developed mapped surfaces showing areas of high selection by multiplying the coefficients for the variables within each seasonal selection model (Tables 3.4, 3.5; Figures 4.2, 4.3) by their appropriate input layers and summing the values. Because the

values are relative to each season and species, they were then scaled between 0 and 1 for comparison among seasons. Each pixel within the mapped surface was given a relative value related to its relative selection. All maps were plotted by quantiles of equal interval (0-0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8, 0.8-1). These seasonal maps showing relative rankings of areas based on resource selection models indicate that areas with the highest selection for wolves tended to be associated with major drainages during all seasons, as well as with eastern boreal flats during denning (Fig. 6.1, 6.2). Areas with characteristics with highest selection value for female grizzly bears were generally on tops of ridges in spring, interspersed throughout the BP during summer, and on slopes bordering prominent valleys in fall (Fig. 6.3).

Habitat Suitability Models and Pre-tenure Planning Zones

Habitat suitability index (HSI) models have been developed by BC Ministry of Environment staff (Rod Backmeyer, Fort St. John) for grizzly bears in spring and for ungulates in winter in the BP. No HSI models have been developed for wolves in the BP. The HSI models were based primarily on literature review and local accounts of high-use areas, and were developed to help rank the Besa-Prophet landscape using classes from 1 (high value) to 6 (low value) during pre-tenure planning processes. Pre-tenure plans (British Columbia Ministry of Sustainable Resource Management 2004) are intended to:

- encourage and guide environmentally responsible development of oil and gas resources by providing results-oriented management direction that ensures oil and gas activities are consistent with the Muskwa-Kechika Management Area Act (MKMA Act);
- provide a sustainable resource management framework to address social well-being, environmental conservation and economic prosperity; and
- identify roles and responsibilities for ongoing monitoring of progress in achieving the results anticipated by the pre-tenure plan.

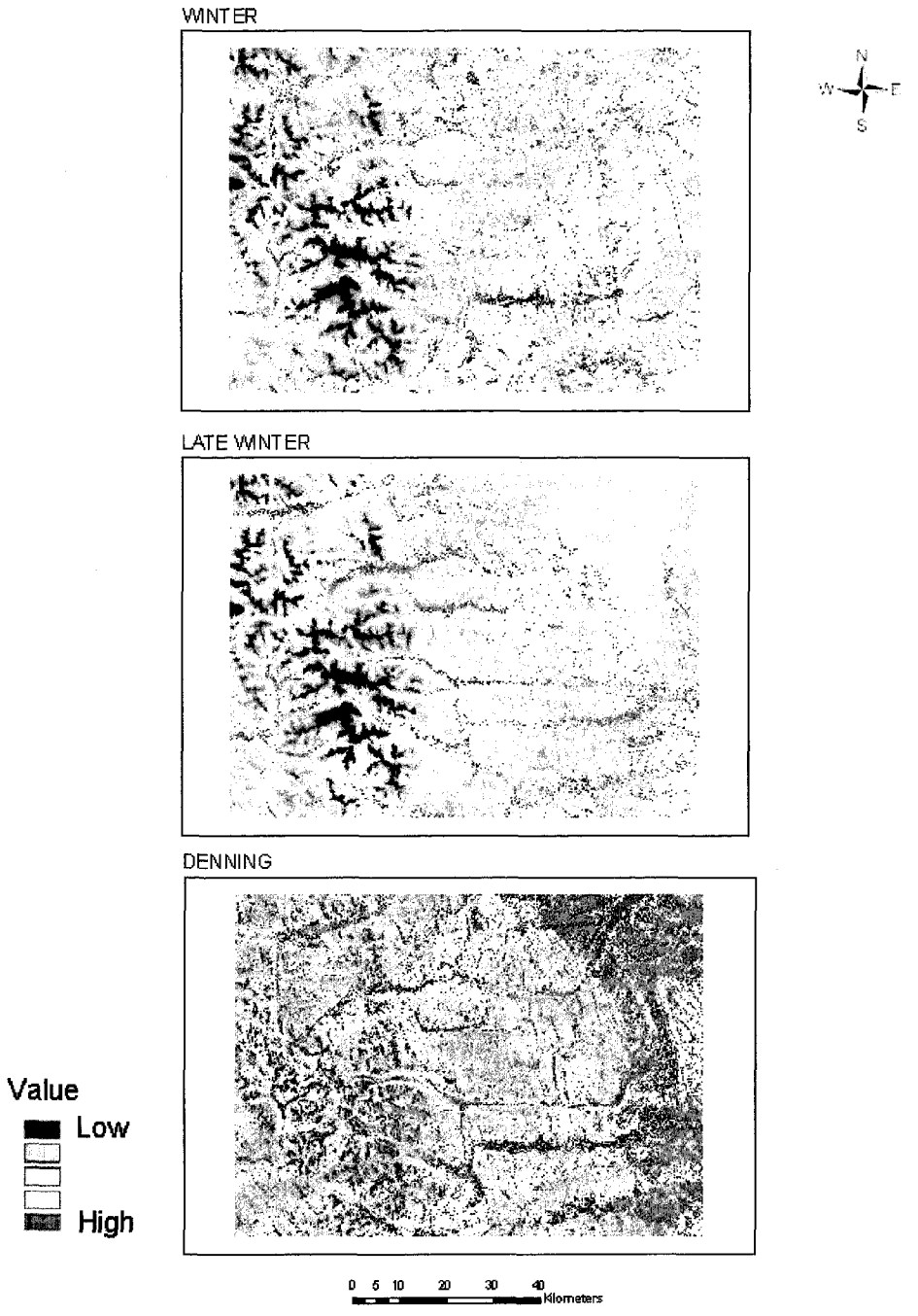

Figure 6.1. Relative habitat selection value for wolves during winter, late winter, and denning in the Besa-Prophet study area based on attributes in resource selection models.

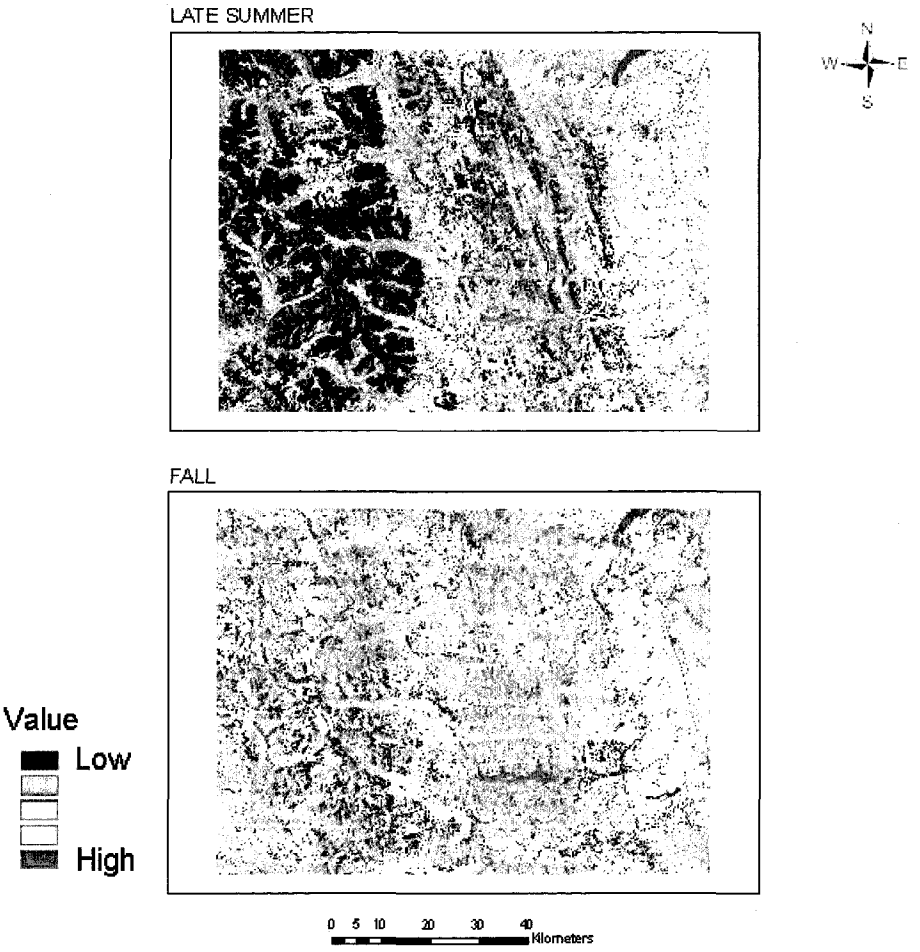

Figure 6.2. Relative habitat selection value for wolves during late summer and fall in the Besa-Prophet study area based on attributes in resource selection models.

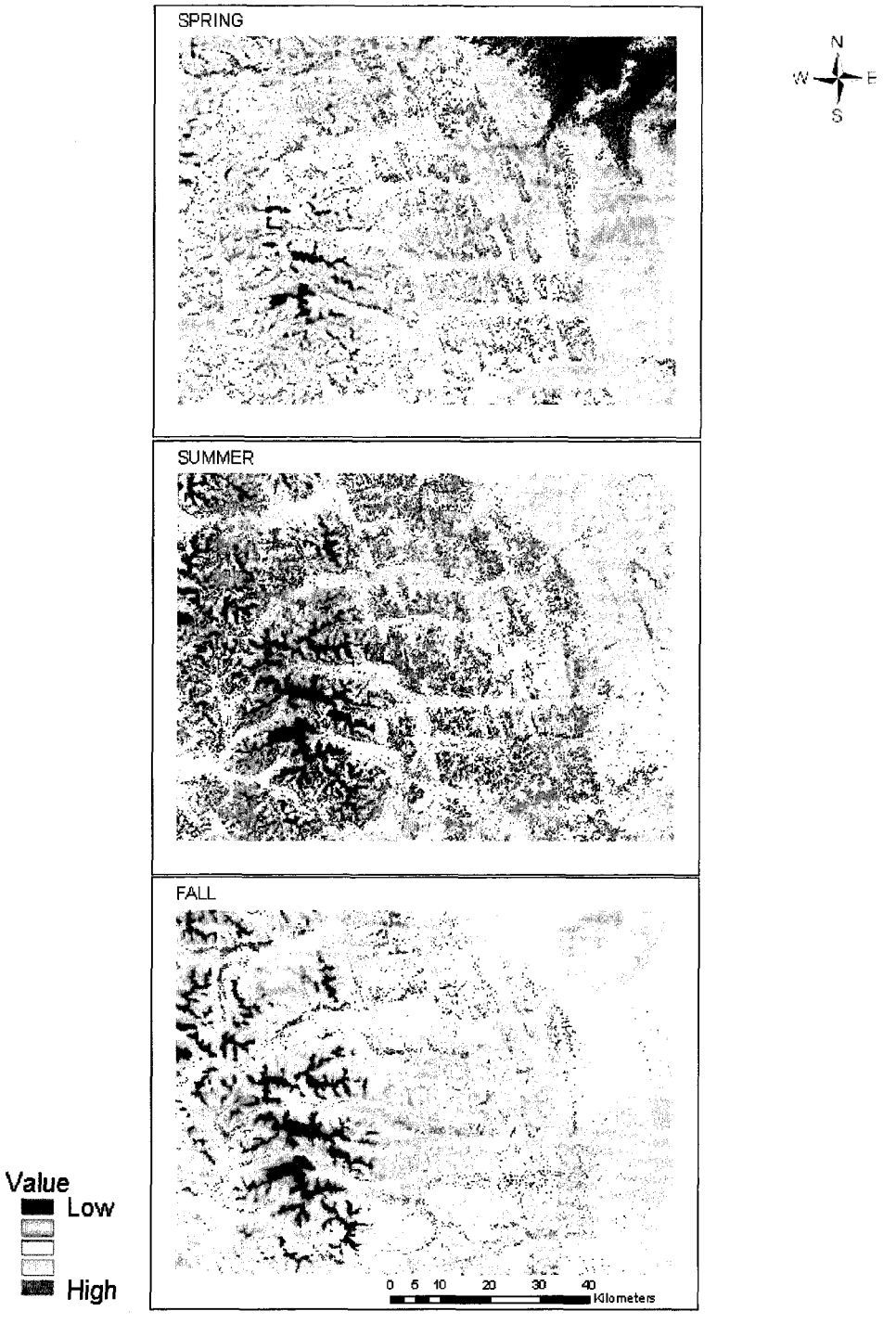

Figure 6.3. Relative habitat selection values for female grizzly bears during spring, summer, and fall in the Besa-Prophet study area based on attributes in resource selection models.

The Besa-Prophet Pre-tenure Plan (British Columbia Ministry of Sustainable Resource Management 2004) incorporates a roll-up map from the HSI modeling efforts on individual species. It categorizes the landscape into zones, as defined by physical and topographical features (Table 6.1). I examined wolf GPS locations during winter relative to the Besa-Prophet Pre-tenure zones which are intended as the management units for oil and gas development. Each zone tried to incorporate conservation value for each species, although management targets may be variable. I also examined wolf GPS locations relative to winter habitat suitability models developed for ungulates to show that these models alone are insufficient to explain wolf distribution and interactions with prey species on the landscape.

Wolves were found in 5 pre-tenure zones over 85% of the time (Fig. 6.4): cool aspect forest (CAF, 15.1%), low elevation wetland (LEW, 15.6%), warm aspect forest (MWA, 14.8%), steep slope cool aspect (SCA, 18.8%), and steep slope warm aspect (SWA, 22.3%). CAF was used in proportion to its availability. This zone is described as a wildlife movement corridor, and the low to moderate slopes typical of the zone may facilitate wolf movements and partially account for wolf use. Both the LEW and MWA zones were used in greater proportion than what was available on the landscape. These zones provide for critical winter moose habitat, and the MWA zone may provide additional critical winter elk habitat. Moose and elk are major prey items in the diets of wolves in the BP as determined by stable isotope analysis (Chapter 5). Both the SCA and SWA zones were used proportionately less than available, likely owing to mountainous terrain and steeper slopes. Nonetheless, ~40% of wolf locations occurred in theses two zones, which provide important wintering habitat for moose and elk. Wolves tended to use areas ranked as high suitability for elk and moose more than would be randomly encountered on the landscape (Fig. 6.5).

Table 6.1. Biophysical zones with wildlife value and management requirements in the pre-tenure planning areas of the Muskwa-Kechika Management Area relevant to the Besa-Prophet study area (British Columbia Ministry of Sustainable Resource Management 2004).

Code	Pre-Tenure Biophysical Zone	Description
LEW	Wetlands – Low Elevation	Concentrated in valley bottoms and lowland areas. Consists of seasonal and year-round moisture saturated soils; watercourses and coniferous/deciduous forest patches can be dispersed throughout the wetland. Contains summer and critical winter habitat for moose, and critical caribou habitat. The wetland zone is important for maintaining water quality and quantity.
HEW	Wetlands - High Elevation	Located in mid to high elevation valley bottoms. Consists of seasonal and year-round moisture saturated soils. Minimal if any coniferous forest within or adjacent to this zone. Contains summer moose habitat, and critical caribou winter habitat.
MOS	Mosaic	Contains a mixture of forested and open habitats interspersed with wetlands, meadows, and forested lowlands and hills. The zone provides a mixture of foraging and security cover for ungulates. It contains critical winter habitat for moose and caribou.
IS	Incised Stream	Consists of steep-sloped stream-banks with flat upland areas. Important values include riparian habitat, wildlife movement corridor and water quality and quantity. A mixture of ungulate security and foraging cover primarily on the uplands with a minor component on the steep slopes. Critical moose and elk winter habitat on the upland region.
MWA	Warm Aspect Forest (moderate <45% slope)	Consists of both extensive tracks of coniferous tree species and open forested habitat on southwest aspect slopes of gentle to moderate sloped terrain and contains areas of old growth. Depending on the pre-tenure plan area, this zone can provide critical winter elk habitat depending on snow depths. Younger willow stands provide critical winter moose habitat. Spring grizzly habitat is found on steeper slopes that experience early snowmelt.
CAF	Cool Aspect Forest (<45% slope)	Consists of wet and cool forests that occur on gentle to moderately sloped terrain. Some forest stands may be interspersed with smaller interconnected wetland complexes. Older forest stands contain critical winter caribou habitat, while shrub areas provide critical moose habitat. This zone is a wildlife movement corridor.

Table 6.1 Continued

SWA	Steep Slope Warm Aspect (>45% slope)	Consists of open and forested habitat on steep, southwest facing slopes. A variety of terrain features and habitat types are found in this zone including: alpine meadows, old growth forested stands, parkland, young forests, cliffs, rock outcrops, and talus slopes. Steeper slopes are primarily open and provide critical winter Stone's sheep habitat and important year round goat habitat. This zone also provides elk and moose winter habitat and birthing and rearing areas for Stone's sheep, mountain goat, and caribou. Higher elevation zones have lower biological productivity.
SCA	Steep Slope Cool Aspect (>45% slope)	Consists of open and forested habitat on steep, northeast facing slopes. A variety of terrain features and habitat types are found in this zone including: alpine meadows, old growth forested stands, parkland, young forests, cliffs, rock outcrops, and talus slopes. This zone is primarily mountainous terrain, highly visible throughout the plan area. Critical winter Stone's sheep habitat borders a large portion of this zone. Steep slopes offer security habitat for caribou, elk, and moose. This zone is important as a wildlife movement corridor, and for grizzly bear denning. Higher elevation zones have lower biological productivity.
HEP	High Elevation Plateau	Consists of high elevation plateaus, often surrounded by steep open and treed terrain. The plateaus are primarily open and consist of vegetation types that are particularly sensitive to disturbance due to low biological productivity, shallow soils, and low moisture and nutrient conditions. Isolated pockets of coniferous forest are found on some plateaus. These areas are prone to strong winter winds and provide critical winter caribou habitat especially during winters of high snowfall.
RFP	Major River Floodplain	A low elevation zone characterized by braided streams bordered by a multi-layered forest canopy and understory. Waterflow varies throughout the year with peak flows generally occurring late spring and early summer. Year to year, the active water channel can change location within the floodplain. The zone provides foraging, security, and thermal cover for elk, moose, and grizzly bear.

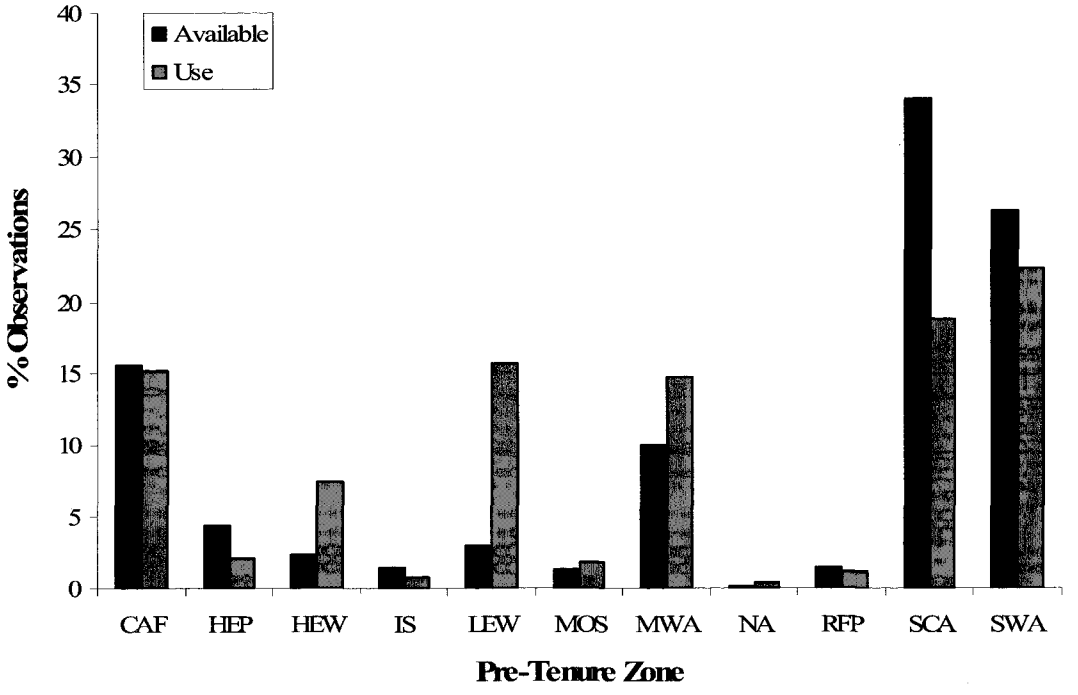

Figure 6.4. Winter and late winter GPS locations (n = 1695) of radio-collared wolves in the Besa-Prophet Pre-tenure Planning Area in relation to zones designated in the Besa-Prophet Pre-tenure Plan. Pre-tenure zones as defined in Table 6.1 are shown as % area of the Besa-Prophet Pre-tenure Planning Area.

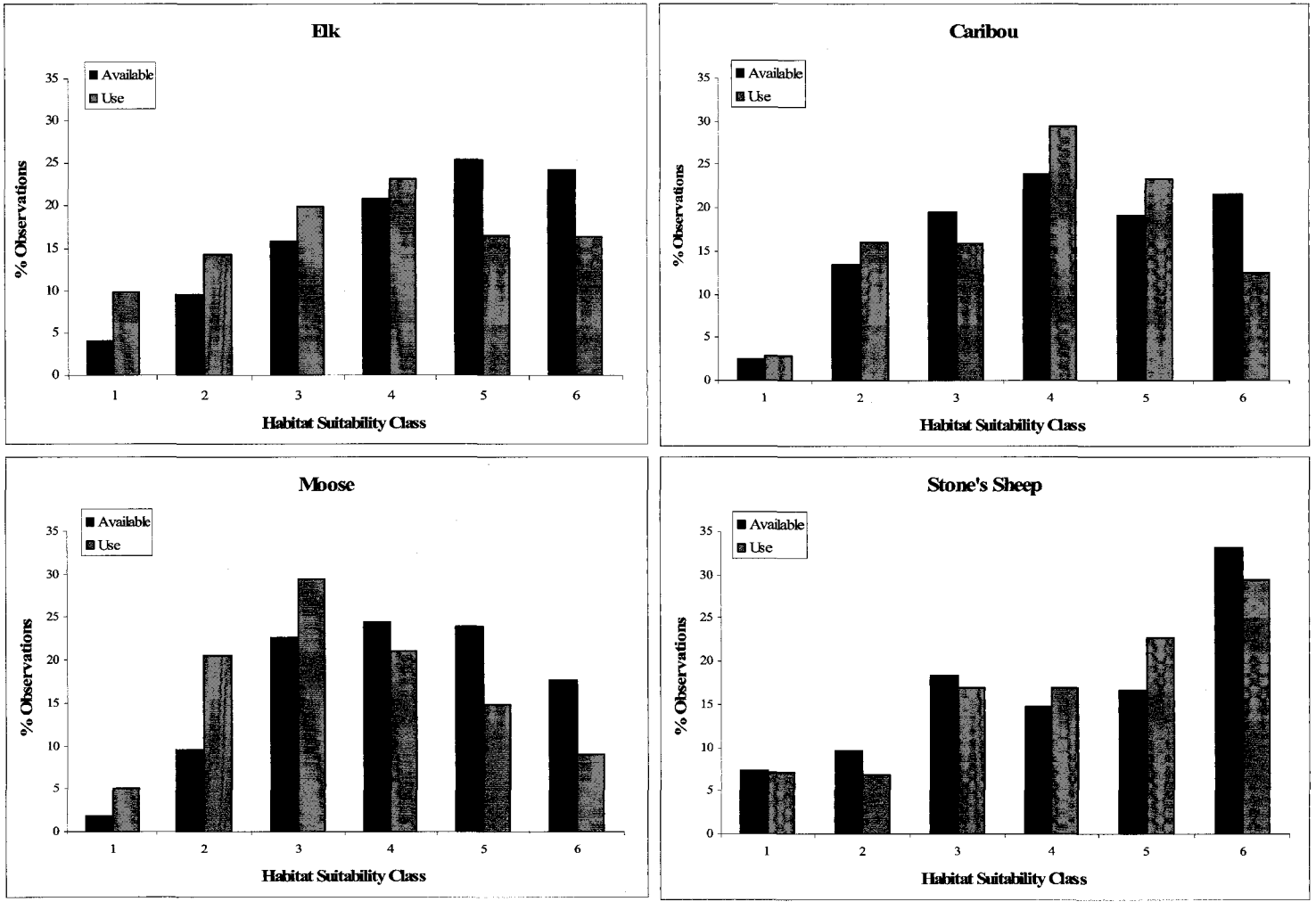

Figure 6.5. Winter GPS locations (n = 1695) of radio-collared wolves in the Besa-Prophet Pre-tenure Planning Area, in relation to availability of winter habitat suitability classes for elk, caribou, moose, and Stone's sheep (habitat suitability information provided by BC Ministry of Environment, Fort St. John, BC).

Selective use of high-value Stone's sheep and caribou habitats across the winter was not as apparent. Similarly to the remotely-sensed layers describing relative habitat quality for prey as variables in the seasonal wolf distribution models (Chapter 3), models based on winter ungulate HSIs did not rank amongst the top models describing winter wolf distribution in the BP.

For the past few decades, expert opinion has formed the basis for wildlife habitat evaluations within the context of such methods as HSI. HSI is an equation of an additive, multiplicative or logical form with coefficients representing the relative value of environmental features. Coefficients are scaled in importance using best available knowledge as surveyed from experts or published literature (Johnson and Gillingham 2004). HSI models rank polygons that incorporate numerous physical and topographical variables such as major plant associations, soil type, moisture regime, and slope, into a single ranking or habitat score. These approaches can be important, particularly for areas with few available data, but are rarely validated, and initiatives designed to deter the decline, extirpation, or extinction of a species often cannot wait for the outcomes of empirical studies (Johnson and Gillingham 2004). However, uncertainty inherent in HSI approaches can have dramatic effects on model predictions and ultimately conservation and management actions (Johnson and Gillingham 2004). In comparing numerous techniques that are available to describe species distributions, Johnson and Gillingham (2005) concluded that generalized linear models, including resource selection functions derived from logistic regression, offer the greatest flexibility in model construction.

I also examined spring habitat use by female grizzly bears in relation to the Besa-Prophet Pre-tenure zones (Fig. 6.6). More than 82% of all spring locations were located in the steep slope cool aspect (SCA) and steep slope warm aspect (SWA) zones. The SWA was used more frequently than would be predicted based on availability. The warmer southern aspects, steeper slopes, and diversity of habitat types and terrain features found in the SWA zone probably provide extensive foraging opportunities and security cover for cubs, and these areas are often snow-free earlier than other zones. The SCA zone was used proportional to availability. Grizzly bears may be able to surprise ungulates that utilize the SCA zone as security cover. This zone is also considered favorable for grizzly bear denning (see Appendix E, Table E1) because northeast-facing slopes may provide deeper snow depths and insulation during the winter months. Female grizzly bears in the BP in spring used higher value habitats, as ranked by spring HSI modeling, proportionately more than what were available on the landscape (Fig. 6.7). Almost 2/3 of all locations were recorded in suitability classes 2 and 3. Spring HSI models for grizzly bears in the BP are based on Terrestrial Ecosystem Mapping (TEM), an expert-based approach to habitat modeling that is based on air-photo interpretation and field checks, and may be supplemented with additional data sources (Sims 1999). These models were developed from the perspective that abundance and availability of food are the most important factors determining habitat selection by grizzly bears, and spring may be most critical to bears as body condition is poorest and spring forage may be limiting (Sims 1999). The models are developed in relation to provincial benchmarks (Fuhr and Demarchi 1990). The BP does not contain the best habitat in comparison to provincial benchmarks (i.e., class 1), but this is not to suggest that the BP contains only moderate habitat for grizzly bears. Classes 2 and 3 may be

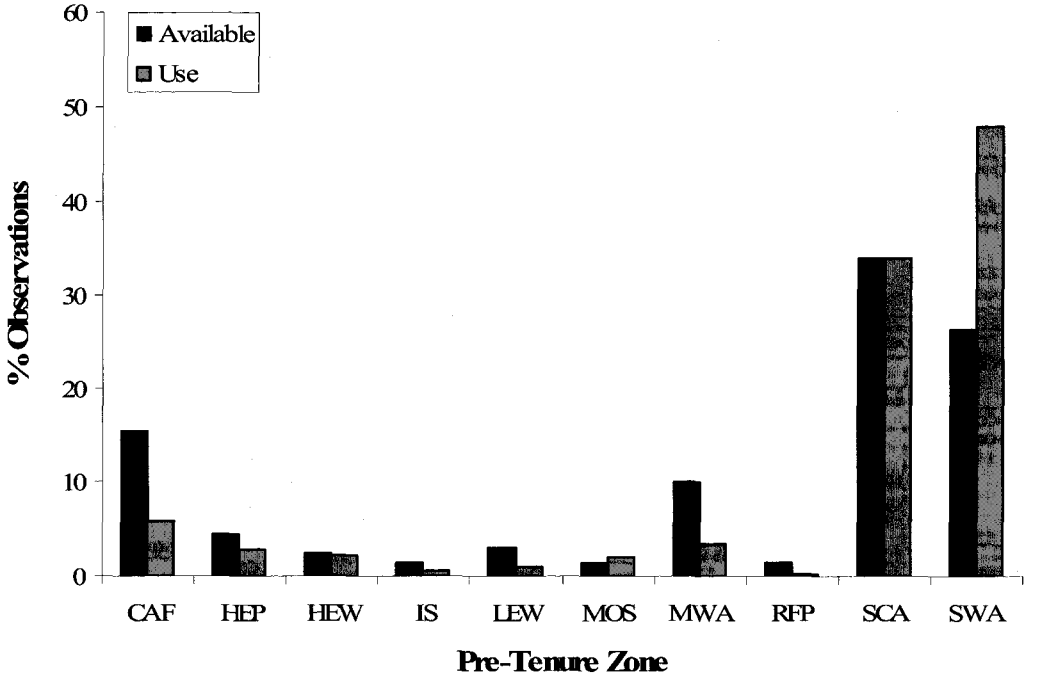

Figure 6.6. Spring GPS locations (n = 1859) of radio-collared grizzly bears in the Besa-Prophet Pre-tenure Planning Area in relation to zones designated in the Besa-Prophet Pre-tenure Plan. Pre-tenure zones as defined in Table 6.1 are shown as % area of the Besa-Prophet Pre-tenure Planning Area.

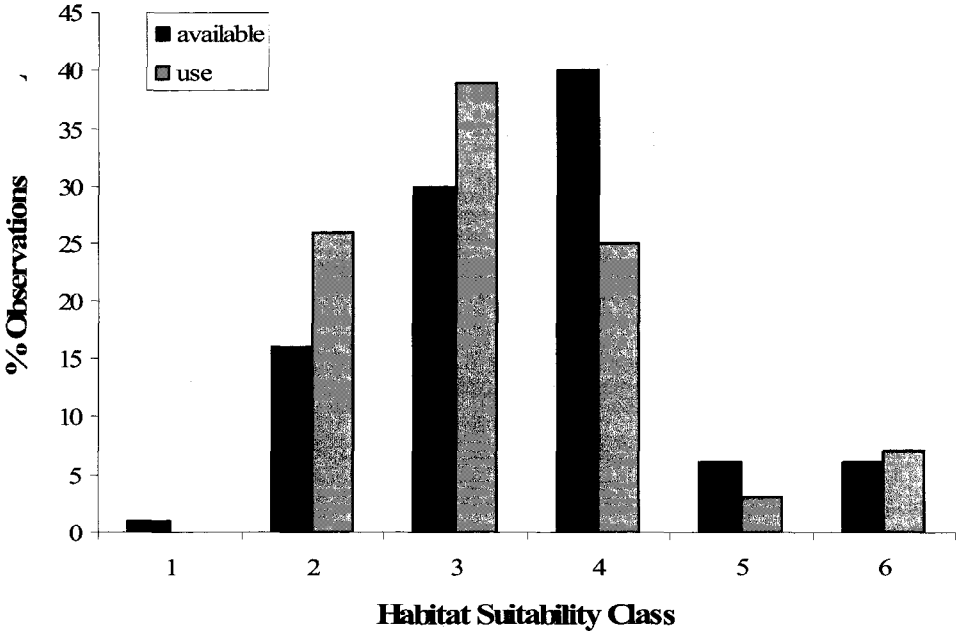

Figure 6.7. Spring GPS locations (n = 1859) of radio-collared grizzly bears in the Besa-Prophet Pre-tenure Planning Area, in relation to availability of spring habitat suitability classes (provided by BC Ministry of Environment, Fort St. John, BC).

moderate in terms of provincial habitat rankings, but for this population, these classes are significant. Similarly, HSI was ineffective at identifying high quality class 1 habitats for BC's Wolverine Caribou Herd during early winter, which was a function of the bench-marking procedure designed to rank habitats across the study area in relation to the best woodland caribou habitat in BC (Johnson and Gillingham 2005). The authors concluded that such an approach allows planners and managers to assess the value of habitats among individual mapping projects and geographic areas, but fails to recognize the relative significance of habitats within populations. Wildlife habitat ratings are a relative measure of a particular ecological unit's capacity to support a species compared with the best available habitat for that species across BC, but the concept is vague given the reliance on subjective provincial benchmarks as opposed to a well-defined measurable parameter (Johnson and Gillingham 2004).

Biogeoclimatic Zones

I examined seasonal habitat use by wolves and grizzly bears in relation to the BC biogeoclimatic ecosystem classification (BEC) zones and sites series, as used in TEM modeling because I wanted to explore the utility of this method in describing predator distributions. TEM uses traditional cartographic methods to stratify landscapes into map units (polygons) which are based on the relationships between ecological features such as climate, physiography, surficial material, bedrock geology, soil and vegetation (British Columbia Resources Inventory Committee (RIC) 1998). TEM maps supply information that may be useful for land-use planning and wildlife habitat management. Ecosystem mapping combines aspects of BC's BEC descriptions with aspects of ecoregion classification.

Ecosystem mapping is based on a classification system delineated by ecoregion units, biogeoclimatic units, site series, and vegetation developmental stages (British Columbia Resources Inventory Committee (RIC) 1998). Ecosystems are mapped using a procedure that focuses on observable site and biological features assumed to determine the function and distribution of plant communities on the landscape (British Columbia Resources Inventory Committee (RIC) 1998). In a hierarchical fashion, BEC represents a multi-ecosystem unit description of climate, site and soil conditions; site series describes climax vegetation for a particular ecosystem unit; structural stage represents the successional stage of the ecosystem unit; and site modifier describes atypical occurrences of the site series with respect to variation in topography, moisture, soil and soil characteristics (sic. Johnson and Gillingham 2004).

TEM mapping of the BP was conducted between 1997 and 1999 using air photos taken in 1986 and supplemented with Landsat TM and SPOT satellite imagery acquired in September 1997 (Sims 1999). The BP contains 2 ecosections (Meidinger and Pojar 1991): the Muskwa Foothills (MUF) in the east and the Eastern Muskwa Ranges (EMR) to the west. The MUF is an area of lower elevation mountains, isolated by wide valleys. It is in the rainshadow of the Muskwa Ranges, and is commonly influenced by cold Arctic winter air. The EMR includes high rugged mountains, especially in the western portions of the BP. The EMR receives more snowfall than the MUF. Within these ecosections, there are 3 sub-zones in the BP (Meidinger and Pojar 1991): BWBS, SWB, and AT. The boreal white and black spruce (BWBS) at lower elevations has predominantly white spruce and aspen with a dominant stepmoss forest floor (seral stands containing pine and aspen are very common). The spruce-willow-birch (SWB) has 2 variants. At lower elevations, the moist cool variant

(SWBmk) consists of mixed white spruce and sub-alpine fir forests, with bog birch and shrub willow present in the understory. At higher elevations, the moist cool scrub variant (SWBmks) is dominated by lush forb alpine grass communities, in association with shrubby willow, scrub birch and krummholz vegetation (mostly subalpine fir). The Alpine Tundra (AT) zone, generally above 1600 m, has a harsh climate and a very short growing season. At its lower elevations, AT vegetation is dominated by lush mixed forbs and alpine grasses; at higher elevations, growing conditions permit only a less vigorous mix of sedges, dwarf shrubs, forbs and alpine grasses. Site series were grouped by sub-zones and variants, but site modifiers such as soil moisture regime and seral stage were not included in the overall groupings for this analysis. TEM classes for the Besa-Prophet area are presented in Table 6.2. I included only those classes with ≥1% of total locations in the frequency distributions for wolf and grizzly bear locations.

Use of biogeoclimatic zones by wolves was highly variable (Fig. 6.8). Across seasons wolves were found most frequently in the Grey-leaved willow–Scrub birch community in both the MUF and the EMR. During winter, over 1/3 of all locations were recorded in Grey-leaved willow–Scrub birch in both the MUF and EMR ecosections, as well as Willow–Crowberry in the EMR and Willow–Bog birch–Sedge in the MUF. By late winter, nearly 1/4 of wolf locations were in Grey-leaved willow-Scrub birch (Fig. 6.9). Wolves used Currant-Horsetail most frequently during denning, whereas Willow-Bog birch-Sedge was used most often during late summer (Fig. 6.10). In fall, the classes that were used most frequently by wolves included Mountain avens-Arctic lupine and Mountain arnica-Subalpine daisy meadow in the EMR along with Willow-Bog birch-Sedge and Willow-Sedge wetland in the MUF.

Table 6.2. Vegetative communities identified by site series during Terrestrial Ecosystem Mapping (TEM) in the Besa-Prophet study area (Sims 1999).

Site Series	Additional Site Description
Mountain arnica-Subalpine daisy meadow	Lower to upper meso slopes and level, deep, medium-textured soils
Talus	Angular rock formations of any size accumulated at the foot of steep rock slopes as a result of successive rock falls. It is a type of colluvium
Mountain avens-Arctic lupine	Significant slope, warm aspect; shallow soils over bedrock, coarse-textured soils; herb-dominated community
Arctic lupine-Step moss	Gentle slope, deep medium-textured soils
Grey-leaved willow-Scrub birch	Gentle slope, deep medium-textured soils
Willow-Crowberry	Significant slope, cool aspect; deep medium-textured soils
Willow-Sitka valerian	Gentle slopes; deep, medium-textured soils, moist shrub units
Juniper-Wildrye	Significant slope, warm aspect, deep, medium-textured soils
Willow-Bog birch-Sedge	Organic wetland
Willow-Step moss	Gentle slope; deep medium-textured soils
Scrub birch-Bluejoint	Significant slope, cool aspect; deep medium-textured soils
Shrubby cinquefoil-Horsetail	Gentle slope, deep, coarse-textured soils
Willow-Mountain sagewort	Significant slope; cool aspect; deep, medium-textured soils
Fescue-Arctic lupine	Upper, crest position; shallow, rapidly drained, medium-textured soils

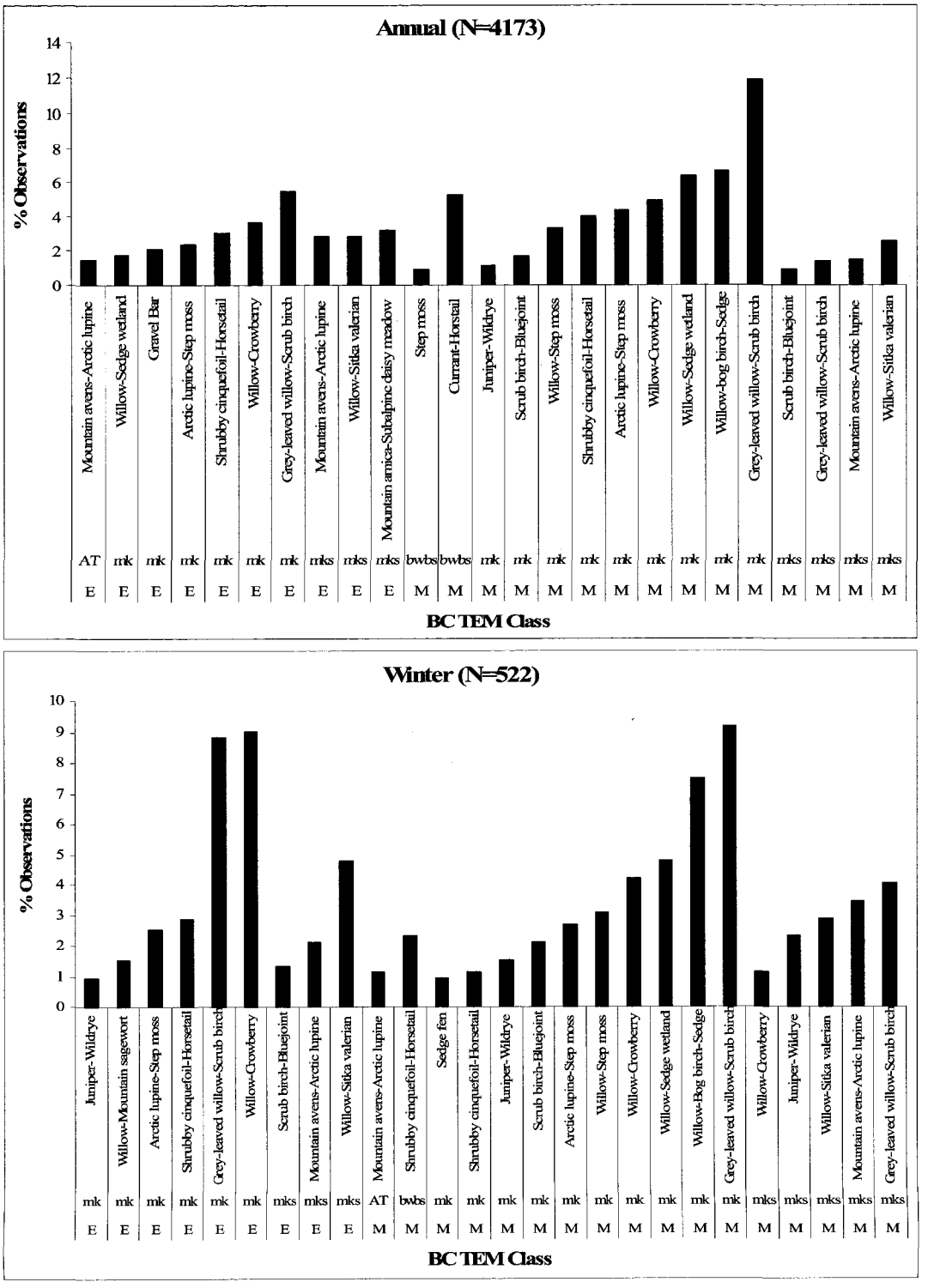

Figure 6.8. Wolf annual and winter habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2002-2004. E refers to EMR (Eastern Muskwa Ranges) and M refers to MUF (Muskwa Foothills) ecosections. All classes are within the spruce-willow-birch (SWB) sub-zone, unless prefixed with AT (alpine tundra) or BWBS (boreal white and black spruce), and separated between the mk (moist cool) and mks (moist cool scrub) variants.

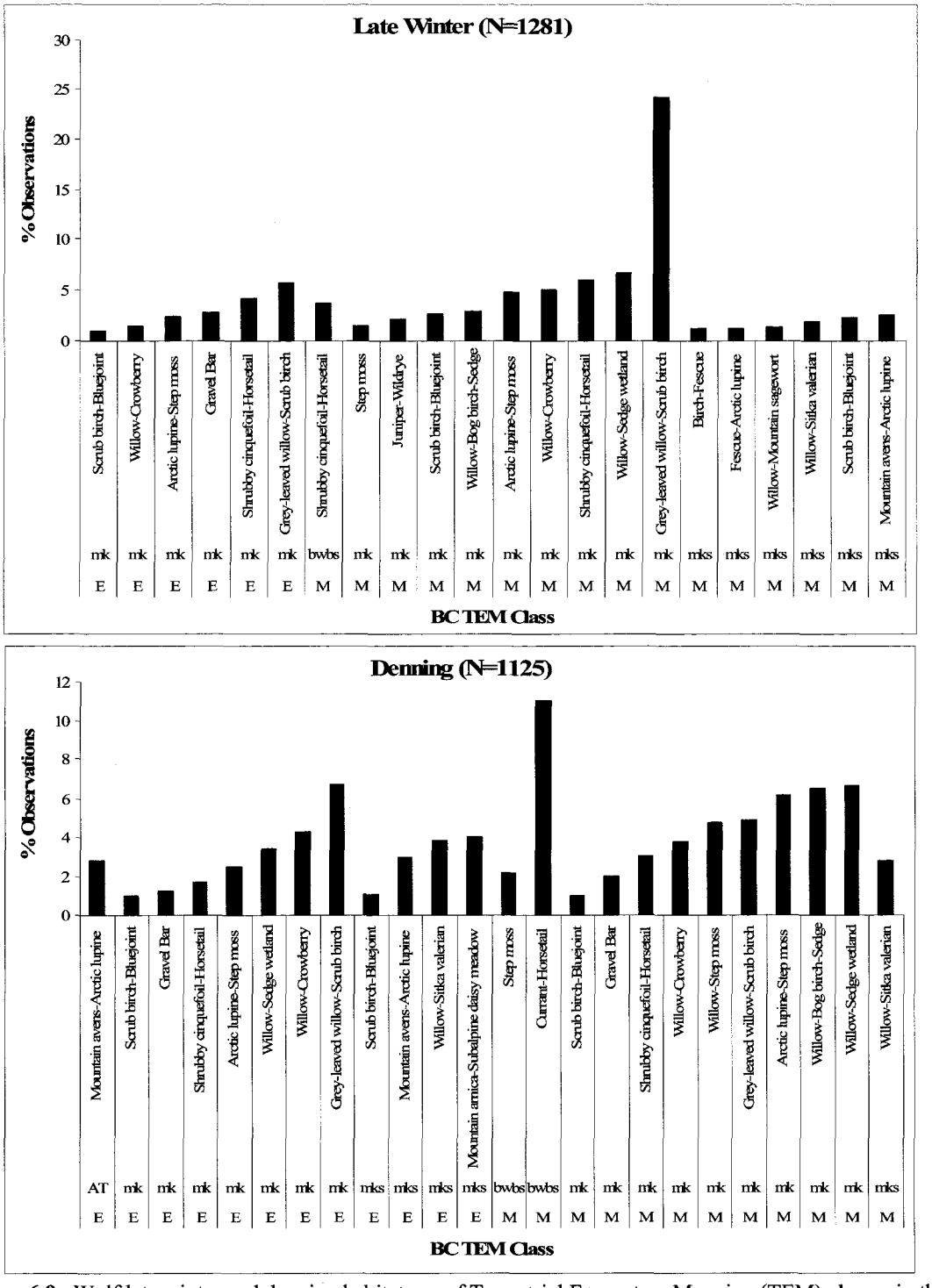

Figure 6.9. Wolf late winter and denning habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2002-2004. E refers to EMR (Eastern Muskwa Ranges) and M refers to MUF (Muskwa Foothills) ecosections. All classes are within the spruce-willow-birch (SWB) sub-zone, unless prefixed with AT (alpine tundra) or BWBS (boreal white and black spruce), and separated between the mk (moist cool) and mks (moist cool scrub) variants.

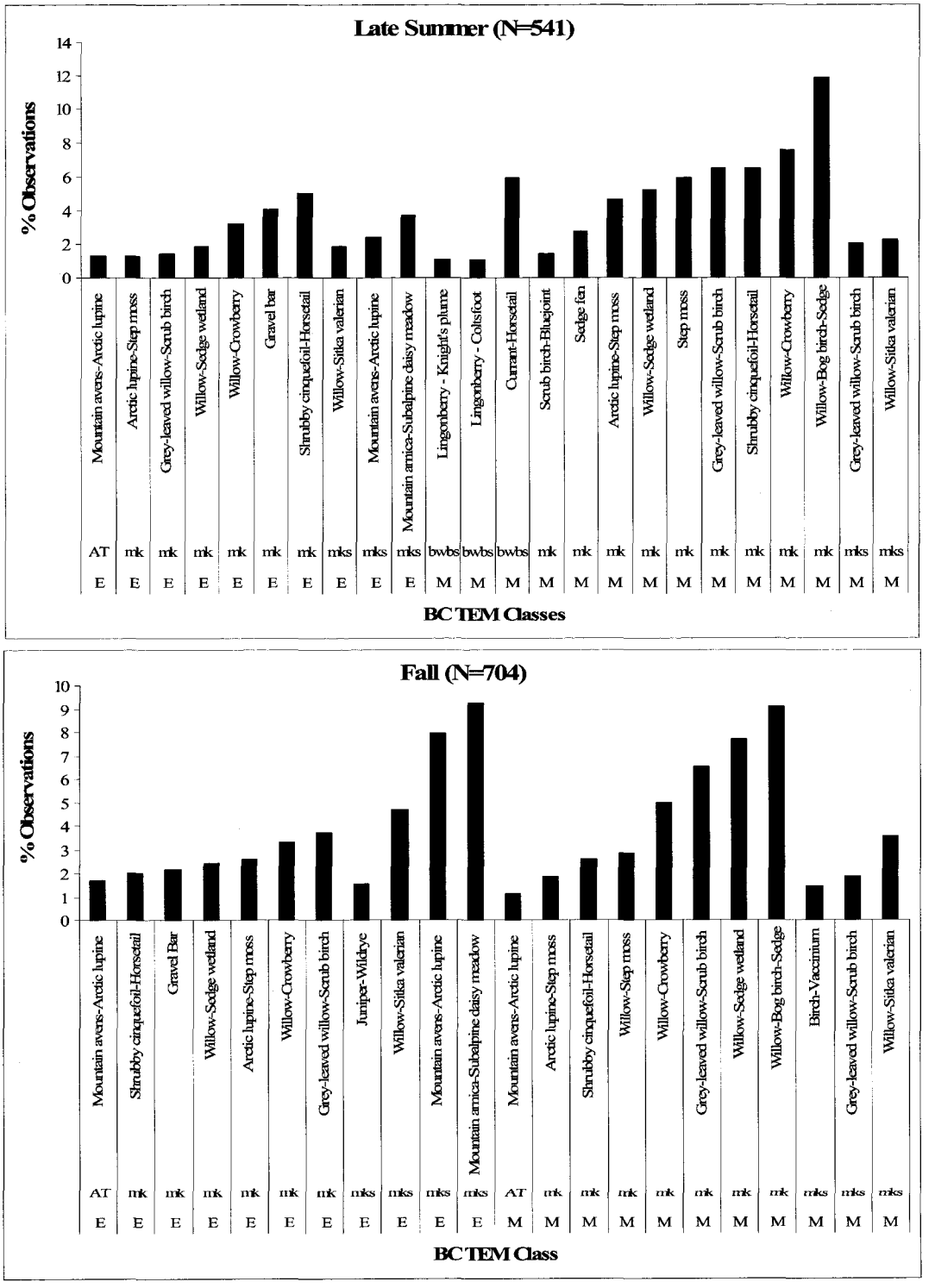

Figure 6.10. Wolf late summer and fall habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2002-2004. E refers to EMR (Eastern Muskwa Ranges) and M refers to MUF (Muskwa Foothills) ecosections. All classes are within the spruce-willow-birch (SWB) sub-zone, unless prefixed with AT (alpine tundra) or BWBS (boreal white and black spruce), and separated between the mk (moist cool) and mks (moist cool scrub) variants.

When pooled across years and seasons (Fig. 6.11), female grizzly bears in the EMR were found most often in Mountain avens-Arctic lupine habitat. In the MUF, Willow-Sitka valerian and Grey-leaved willow-Scrub birch habitats were used most often by bears. During spring (Fig. 6.11), bears in the EMR were in alpine tundra (AT) habitats nearly 10% of the time. Willow-Crowberry, Grey-leaved willow-Scrub birch, and Mountain avens-Arctic lupine habitats also appeared important to bears in the EMR, whereas bears in the MUF were found most often in Willow-Sitka valerian. During the summer (Fig. 6.12), illow-Sitka valerian appeared important to bears in both the EMR and MUF. Mountain arnica-Subalpine daisy meadow and Mountain avens-Arctic lupine habitats were used most in summer by bears in the EMR, whereas bears in the MUF were found 10% of the time in Grey-leaved willow-Scrub birch habitat. Fall use of TEM classes was variable (Fig. 6.12). During this time, bears appeared to favor predominantly Grey-leaved willow-Scrub birch habitat (~20% of locations) in the MUF zone.

Highest overlap in use of TEM classes between wolves and grizzly bears across seasons was in the Grey-leaved willow-Scrub birch class in the MUF. Highest seasonal overlap occurred in late winter/spring, also in Grey-leaved willow-Scrub birch.

Habitat Selection Using Remote Sensing versus HSI Modeling

Besa-Prophet Pre-tenure Planning Zones have limited conservation application for large predators in the BP because they represent coarse spatial scales that incorporate numerous habitat types and terrain features with different conservation implications to different species. In contrast, HSI models focus on a single species during a particular time

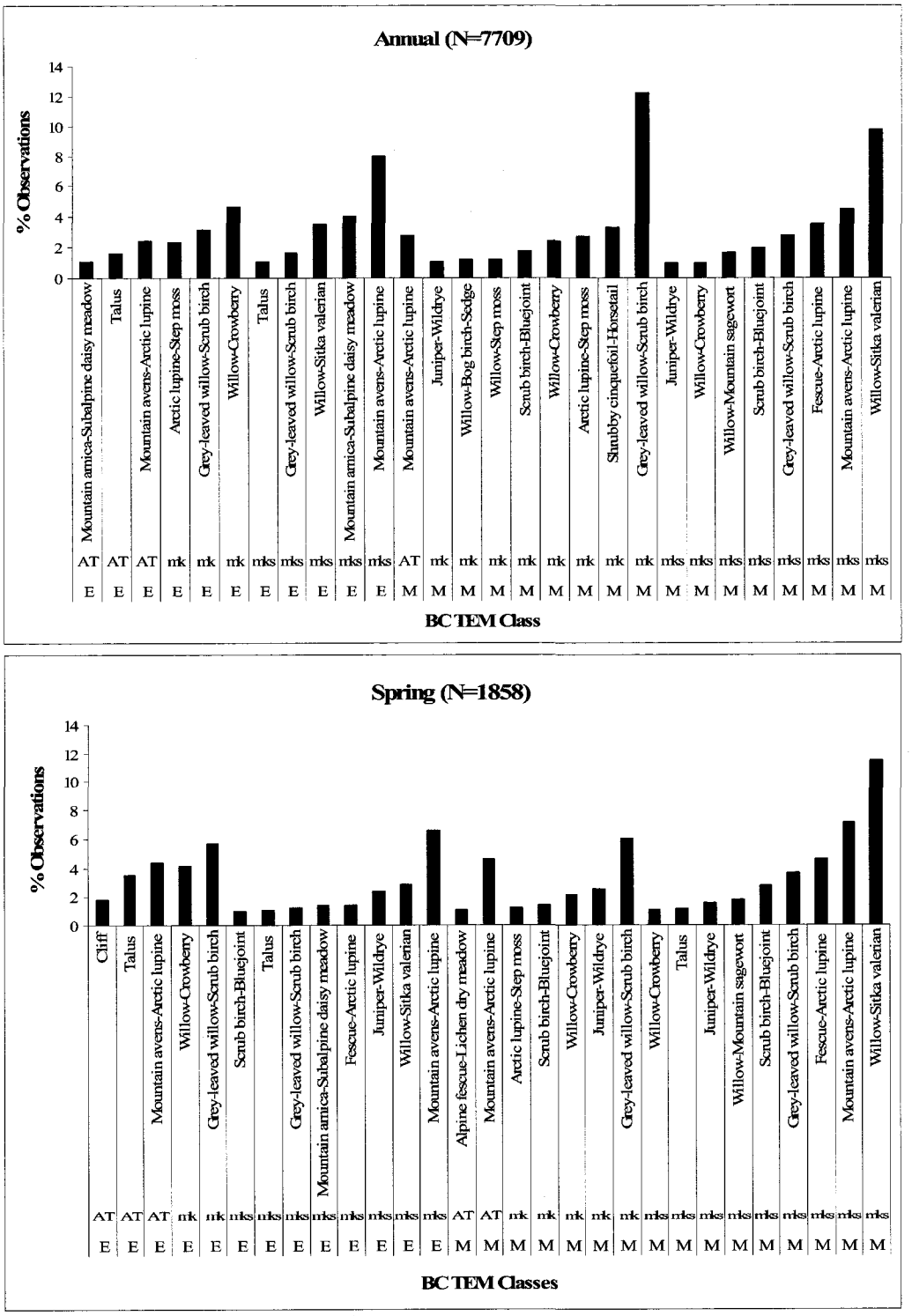

Figure 6.11. Grizzly bear annual and spring habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2001-2004. E refers to EMR (Eastern Muskwa Ranges) and M refers to MUF (Muskwa Foothills) ecosections. All classes are within the spruce-willow-birch (SWB) sub-zone, unless prefixed with AT (alpine tundra) or BWBS (boreal white and black spruce), and separated between the mk (moist cool) and mks (moist cool scrub) variants.

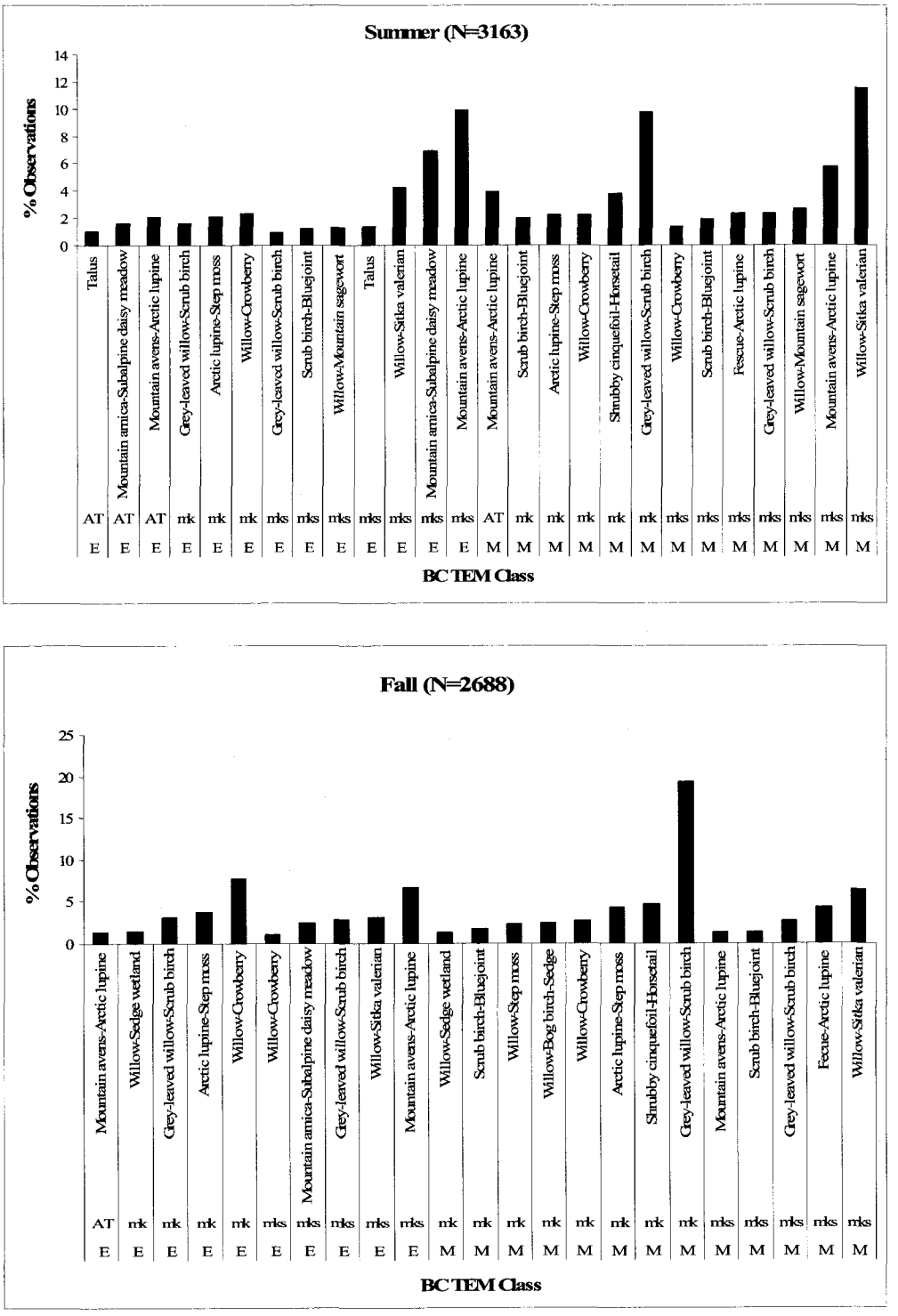

Figure 6.12. Grizzly bear summer and fall habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2001-2004. E refers to EMR (Eastern Muskwa Ranges) and M refers to MUF (Muskwa Foothills) ecosections. All classes are within the spruce-willow-birch (SWB) sub-zone, unless prefixed with AT (alpine tundra) or BWBS (boreal white and black spruce), and separated between the mk (moist cool) and mks (moist cool scrub) variants.

frame that does not provide information on system linkages, and ratings are relative to provincial benchmarks instead of the target population. Beyond assessing the degree to which predators utilize each zone, there is little information as to which habitats or terrain features in particular they are responding to. When examining how predators use individual TEM polygons in the Besa-Prophet, it appears that they spend over 80% of their time in less than 30 pooled TEM polygons. The highest use in specific communities was not a very high percentage given the high number of TEM classes. The TEM classes presented here were already collapsed from hundreds of individual polygons across variants and seral stages. Quality grizzly bear forage may partially be a function of seral stage, but analysis of resource selection or use versus availability that takes into account individual variants and seral stages would require such large samples sizes as to be impractical. Furthermore, inherent to TEM mapping is a high degree of extrapolation across the landscape, and limited field verification of polygon extents that may change on an annual basis. BEC, site series, structural stage and site modifier may be useful for identifying plant associations, but they serve only as vague proxies for factors that dictate wildlife distribution (Johnson and Gillingham 2004).

Although accurate subjective assessments of suitability and broad planning zones may provide general management guidelines, conservation efforts should be based on what animals are using and selecting across the landscape, how these patterns may vary seasonally and annually, and identifying linkages that structure the system. For example, spring HSI models for grizzly bears in the BP are premised on the assumption that spring food drives habitat selection patterns, and that higher quality and quantity of forage may be found at lower elevations during this time (Sims 1999). My results, however, show that

nursing female grizzly bears are found at higher elevations during the spring, which may be related to security cover (Chapter 4). Security cover was ranked as the 3rd (of 5) most important factor to grizzly bears in the BP HSI models (Sims 1999).

Between the extremes of broad planning zones and specific TEM classification, my thesis used a framework for ecosystem planning based on combining GPS locations with remotely sensed imagery of habitat class and other terrain features. With the aid of logistic regression and resource selection functions, the relative selection of habitats and terrain features by predators can be directly quantified, bearing in mind some of the limitations associated with these techniques (Frair et al. 2004; Keating and Cherry 2004; Graves and Waller 2006). The utility of remote sensing is its applicability across scales (e.g., pixel to patch to cover type). Pixels can be combined to generate a suite of habitat classes that are biologically meaningful to the target species or correlate with a biologically meaningful factor, and can be readily identified for managers. I focused on 3rd-order selection by wolves and female grizzly bears in the BP because both maintain relatively stable annual home ranges and the activities of each are based on cyclic annual life-history patterns, such as denning and pup rearing by wolves, or denning by grizzly bears. Once a pack or an individual bear establishes a home range, decisions that are made on a daily and seasonal basis within home ranges directly influence fitness in the short term. Integrating selection patterns across individuals and packs provides detailed information on the distribution of key habitat and terrain features across the landscape, which subsequently provides clearer management and conservation objectives. Although I focused my research on female grizzly bears, which precluded comparisons with males, impacts to female grizzly bears may have greater consequences for the long-term persistence of this population.

Dietary Analyses

Stable isotope analyses showed that moose and elk were seasonally important prey items in the diets of wolves, with additional contributions from caribou and Stone's sheep (Chapter 5). Stable isotopes, in combination with habitat selection information, can provide a clearer understanding of the underlying dynamics that potentially structure communities. For example, at broad scales, wolves often used habitats ranked as high value for moose and elk. Resource selection analysis indicated that wolves selected for shrub and burn-type habitats, which likely improve encounter rates with ungulate prey. Stable-isotope analysis confirmed that wolves were eating moose and elk. Among grizzly bears, males consumed more prey than females and both sexes increased their prey consumption during fall. This increase in meat consumption appeared to be from elk, although it is unknown whether the elk was depredated or scavenged from hunter kills. Prescribed burns for the management of elk and Stone's sheep may be creating additional foraging opportunities for grizzly bears. Regenerating burns and other disturbed areas such as avalanche chutes provide lush, high-quality forage favored by both bears and ungulates. This overlap in highly selected habitats, combined with an increase in elk densities, may result in increased encounters between elk and grizzly bears. Hence the consumption of elk by both wolves and grizzly bears in the BP potentially drive habitat selection patterns that facilitate spatial and/or temporal niche differentiation between the two large predator species. Future research should examine whether grizzly bear prey consumption is predatory in nature, or primarily obtained as carrion. Given densities of grizzly bears in the MUF and EMR ecosections of the Northern Boreal Mountains (~35 bears/1000 km^2) are double what is expected based on provincial habitat capability rankings (Poole et al. 1998), the relative contribution of grizzly bears to

regulating or limiting ungulate populations may be significant if they are predatory. Subsequently, defining dynamics of niche differentiation between grizzly bears and wolves may play an important role in identifying the underlying dynamics that structure the functional and numerical responses of these predators. Significant predation by grizzly bears may require a reexamination of protocols that target wolf management to maintain ungulate populations.

Conclusions

I used GPS technology and remote sensing/GIS tools to demonstrate the relative seasonal value of habitat and landscape features to wolves and grizzly bears. These predators respond to habitats and terrain types within their respective home ranges. As generalist predators and obligate carnivores, wolves are not expected to associate with particular habitat types, but nor is their distribution expected to be random (Mladenoff et al. 1999). Once a territory has been established, wolves may utilize terrain features and habitat types that enable efficient movement through their ranges to facilitate territory defense and to increase encounter rates with preferred prey. Wolves appear to be able to respond quickly to adverse conditions based on my observation of 2 packs shifting their territories to newly vacated areas within a year, apparently in response to den failure.

For omnivorous grizzly bears, the high degree of overlap amongst individual home ranges suggests a productive landscape for grizzly bears. The introduction of industrial development has the potential to exclude bears from seasonally important habitats if access or habitat alteration preclude their use, and to create a landscape where bears more actively compete for increasingly limited resources. Both male and female bears consume substantial amounts of meat, whether predated or scavenged. If predatory, the contribution

to predator-prey dynamics merits further investigation, particularly if industrial development results in significant shifts in species distributions. Prescribed burning activities that were initiated in the 1950's to increase ungulate populations have benefited grizzly bears in this system by creating high-quality forage areas, and potentially increasing encounters with ungulate prey, particularly elk. In addition, my observation that female grizzly bears in the BP used habitats in contrast to those typical of many other interior populations (e.g., staying high during spring) highlights the importance of a better understanding of the distribution of resources for each population, and that without understanding the variability across a population (e.g., sexes, family units) there may be significant repercussions for long-term persistence.

The Besa-Prophet is managed as a multiple land-use region. The objective is to enable access to resources while maintaining wildlife values, or minimally, the potential of the landscape to support diverse large-mammal communities. The information presented in this thesis, in conjunction with concurrent research on Stone's sheep (Walker et al. 2007), caribou (Gustine et al. 2006a,b), moose (Gillingham and Parker 2008a,b), and elk (Gillingham and Parker 2008a) provides a unique opportunity to create a management plan that is proactive and adaptive because it identifies key habitat features used by different species; examines the amount of space used by animals, how they move across the landscape, and how their patterns change seasonally; and defines linkages in the system in terms of predator-prey interactions.

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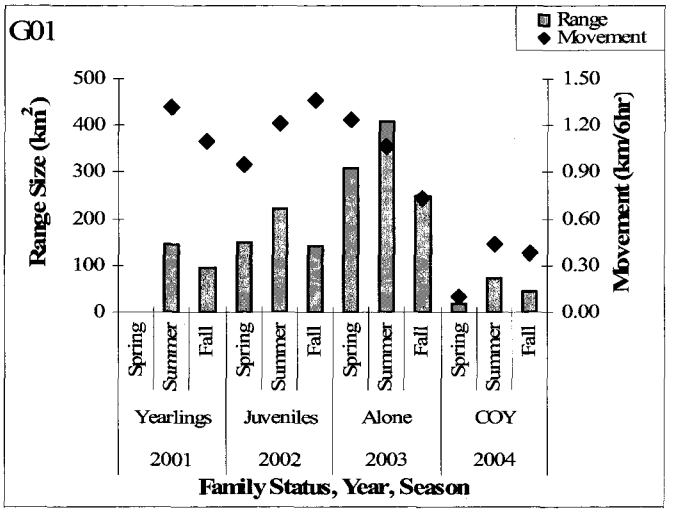
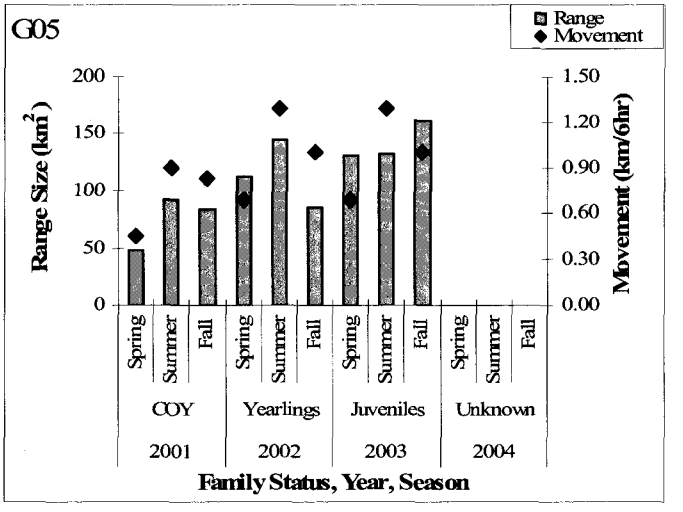
Appendix A: Home range sizes and movement rates of individual grizzly bears and wolf packs in the Besa-Prophet area of northern British Columbia.

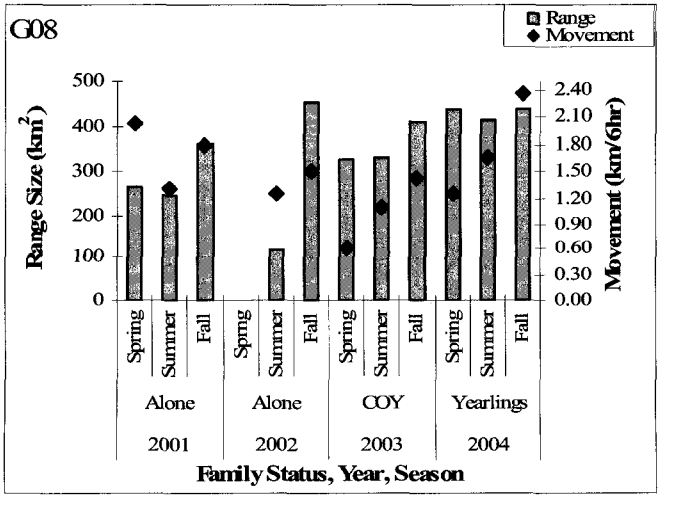
A


G01
Range
Movement
Range Size (km²)
Movement (km/6hr)
500
400
300
200
100
0
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Yearlings
Juveniles
Alone
COY
2001
2002
2003
2004
Family Status, Year, Season

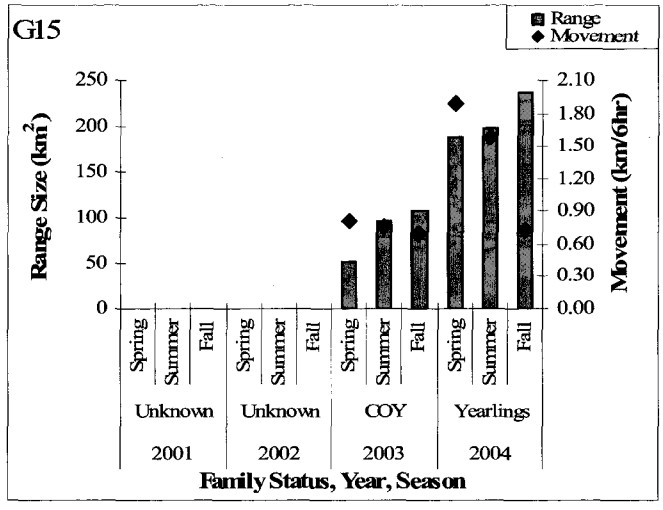
B


G05
Range
Movement
Range Size (km²)
Movement (km/6hr)
200
150
100
50
0
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
COY
Yearlings
Juveniles
Unknown
2001
2002
2003
2004
Family Status, Year, Season

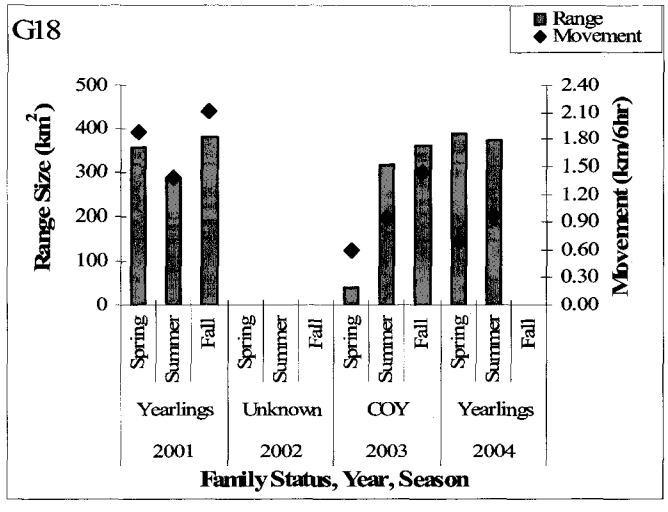
C


G08
Range
Movement
Range Size (km²)
Movement (km/6hr)
500
400
300
200
100
0
2.40
2.10
1.80
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Alone
Alone
COY
Yearlings
2001
2002
2003
2004
Family Status, Year, Season

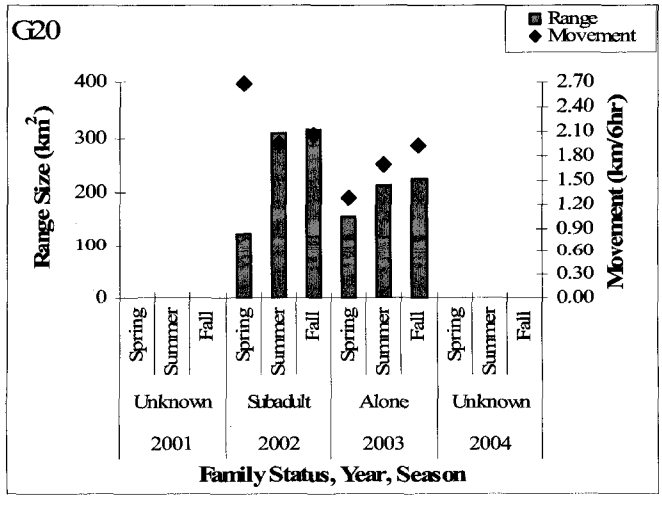
D


G15
Range
Movement
Range Size (km²)
Movement (km/6hr)
250
200
150
100
50
0
2.10
1.80
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Unknown
Unknown
COY
Yearlings
2001
2002
2003
2004
Family Status, Year, Season

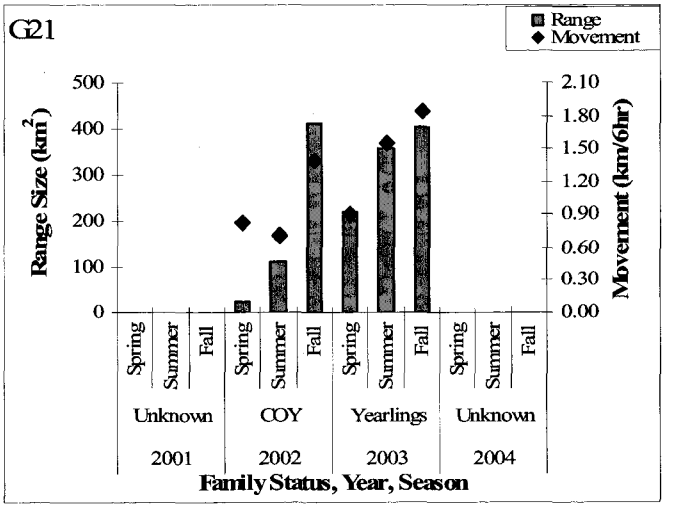
E


G18
Range
Movement
Range Size (km²)
Movement (km/6hr)
500
400
300
200
100
0
2.40
2.10
1.80
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Yearlings
Unknown
COY
Yearlings
2001
2002
2003
2004
Family Status, Year, Season

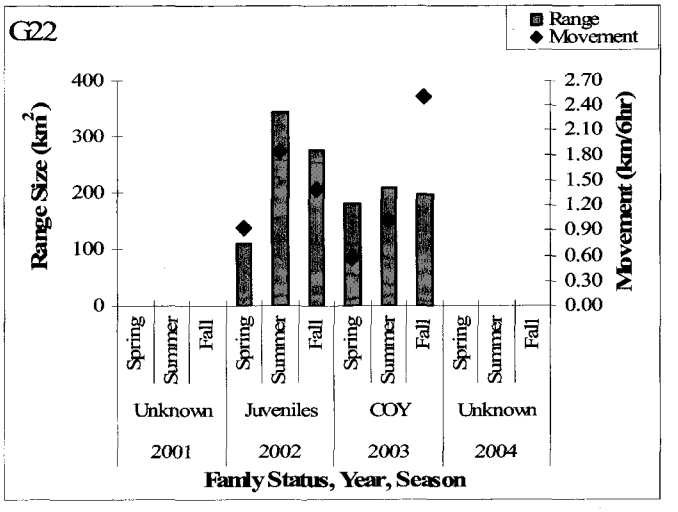
F


G20
Range
Movement
Range Size (km²)
Movement (km/6hr)
400
300
200
100
0
2.70
2.40
2.10
1.80
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Unknown
Subadult
Alone
Unknown
2001
2002
2003
2004
Family Status, Year, Season

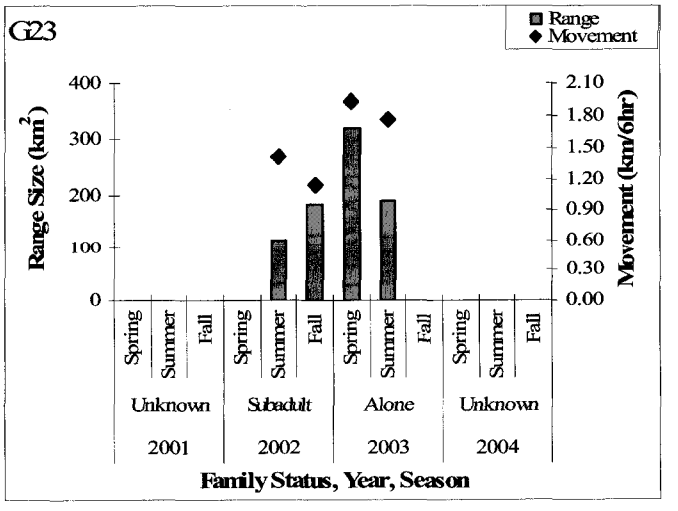
G


G21
Range
Movement
Range Size (km²)
Movement (km/6hr)
500
400
300
200
100
0
2.10
1.80
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Unknown
COY
Yearlings
Unknown
2001
2002
2003
2004
Family Status, Year, Season

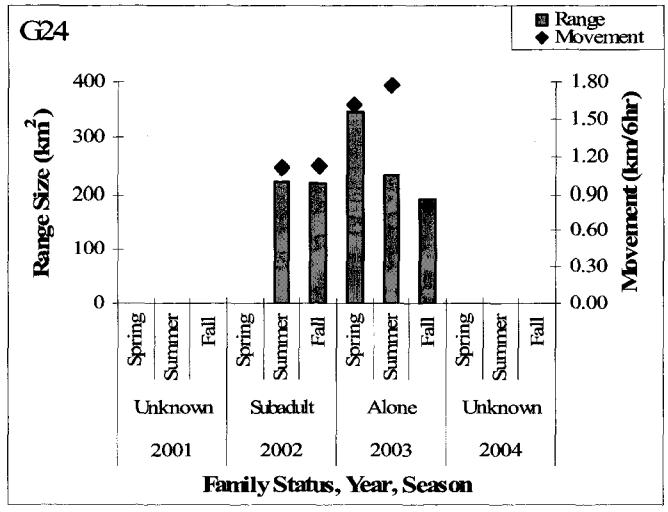
H


G22
Range
Movement
Range Size (km²)
Movement (km/6hr)
400
300
200
100
0
2.70
2.40
2.10
1.80
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Unknown
Juveniles
COY
Unknown
2001
2002
2003
2004
Family Status, Year, Season

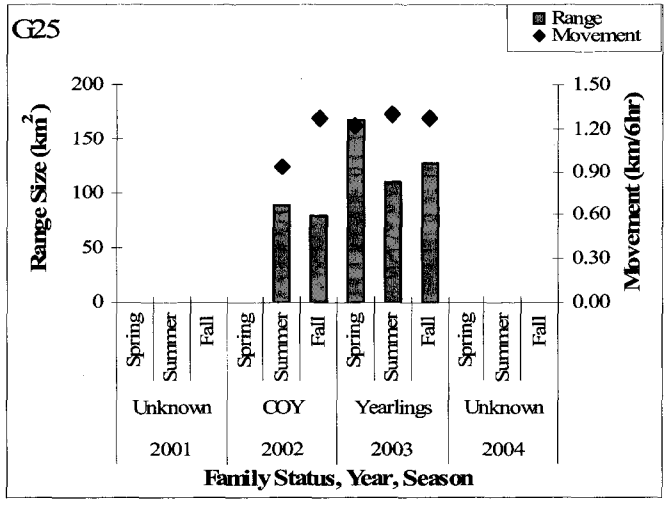
I


G23
Range
Movement
Range Size (km²)
Movement (km/6hr)
400
300
200
100
0
2.10
1.80
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Unknown
Subadult
Alone
Unknown
2001
2002
2003
2004
Family Status, Year, Season

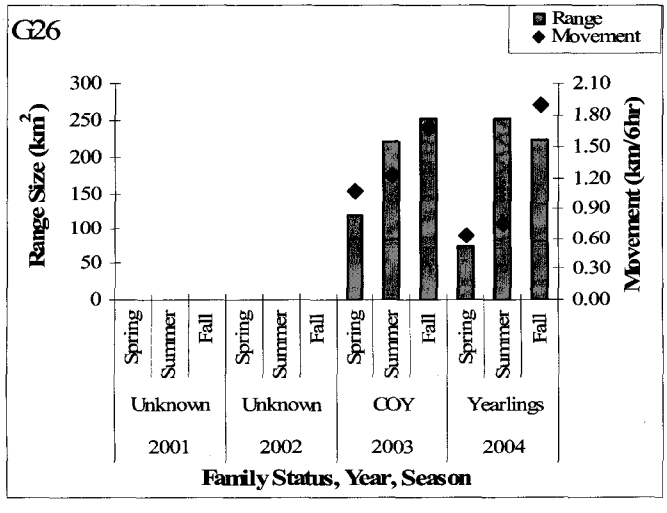
J


G24
Range
Movement
Range Size (km²)
Movement (km/6hr)
400
300
200
100
0
1.80
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Unknown
Subadult
Alone
Unknown
2001
2002
2003
2004
Family Status, Year, Season

K


G25
Range
Movement
Range Size (km²)
Movement (km/6hr)
200
150
100
50
0
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Unknown
COY
Yearlings
Unknown
2001
2002
2003
2004
Family Status, Year, Season

L


G26
Range
Movement
Range Size (km²)
Movement (km/6hr)
300
250
200
150
100
50
0
2.10
1.80
1.50
1.20
0.90
0.60
0.30
0.00
Spring
Summer
Fall
Unknown
Unknown
COY
Yearlings
2001
2002
2003
2004
Family Status, Year, Season

M

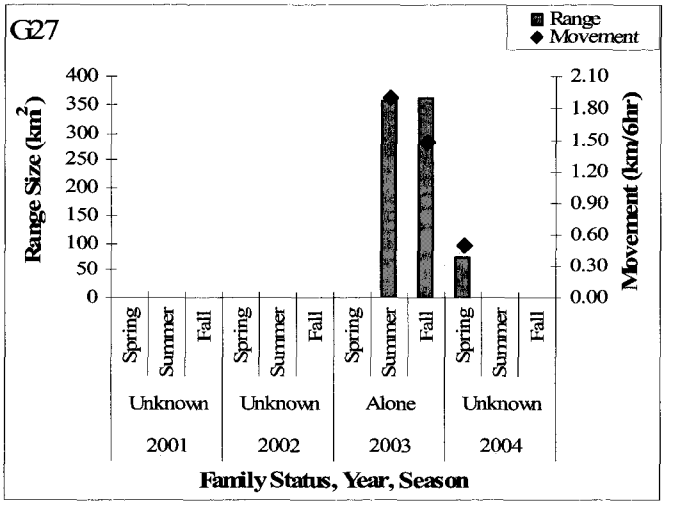


Figure A1 (A-M). Sizes of seasonal home ranges (bars) and movement rates (points) of individual grizzly bears in the BP study area of northeastern British Columbia, by year and family status. COY = cubs of the year, juveniles = 2-year olds.

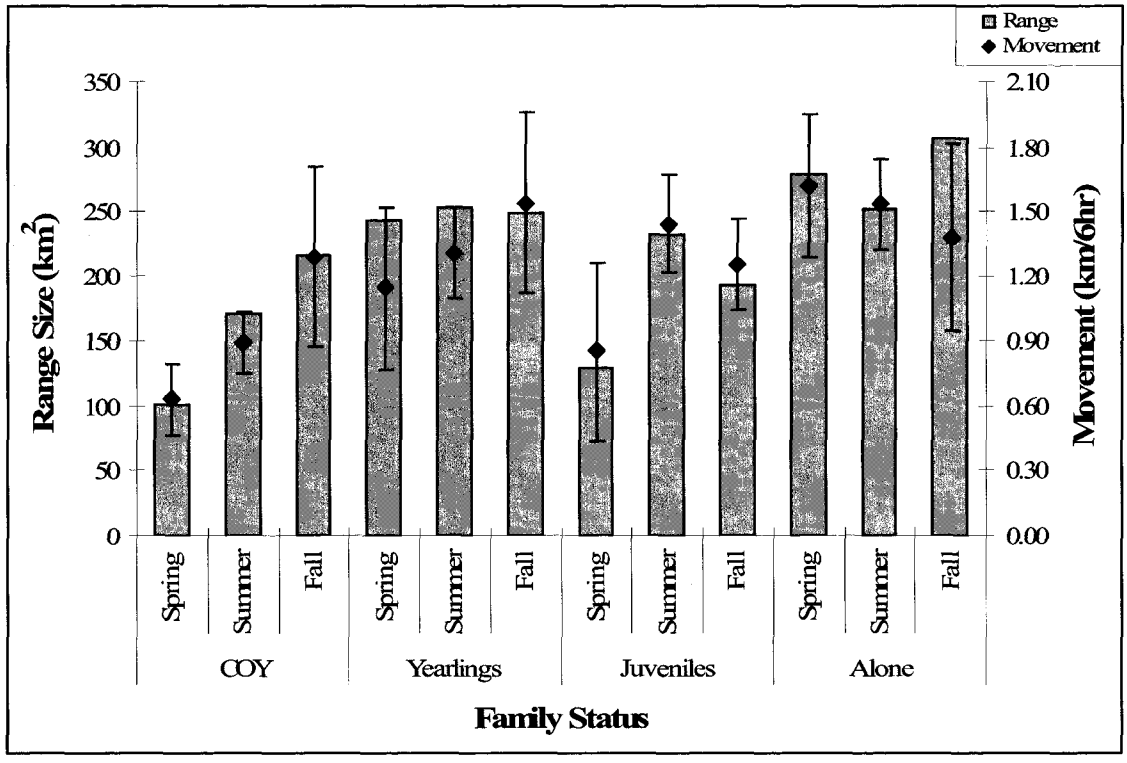


Figure A2. Sizes of seasonal home ranges and movement rates (± SE) of GPS collared female grizzly bears in the Besa Prophet study area. Data are pooled by family status, across years and individuals. COY = cubs of the year (Spring $N = 8$; Summer and Fall $N = 9$); Yearlings (Spring $N = 8$; Summer $N = 9$; Fall $N = 8$); Juveniles = 2-year olds, All Seasons $N = 3$; Alone (Spring $N = 6$; Summer $N = 10$; Fall $N = 9$).

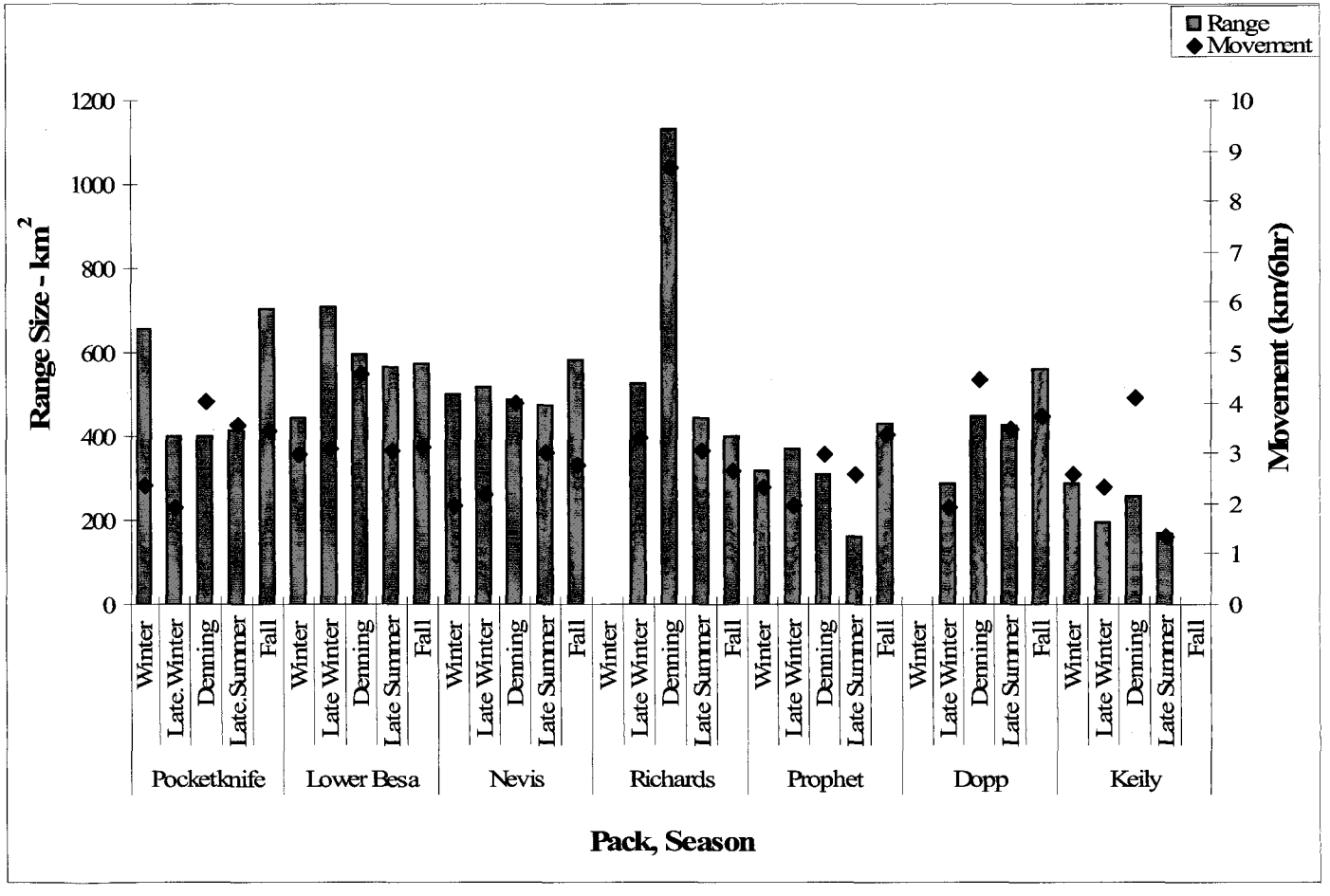


Figure A3. Sizes of seasonal home ranges and movement rates of GPS-collared wolves in the Besa-Prophet study area of northeastern British Columbia, presented by pack.

Appendix B: Final rankings and performance of models used to evaluate selection of resources by wolf packs in the Besa-Prophet area of northern British Columbia. Models were developed across five seasons and from 1-3 years (2002-2004).

Table B1. Seasonal models used in developing surfaces of selection value for potential prey species of wolves in the Besa-Prophet study area, 2001 - 2004. Wolf seasons were paired with the closest corresponding prey seasons for moose (Gillingham and Parker 2008a), woodland caribou (Gustine 2005), and Stone's sheep (Walker 2005). Habitat classes were grouped slightly differently in models for each species. Wolf risk and bear risk are measures of the relative risk of predation from wolves and grizzly bears from a prey perspective. Biomass and quality are indices of vegetation quantity (NDVI) and quality (change in NDVI). Curvature is an overall index of the concavity or convexity of a sampled pixel. Elevation was entered as a quadratic function. Elk layers were obtained from the Conservation Area Design for the Muskwa-Kechika Management Area (Heinemeyer et al. 2004a, b) during the growing (April through October) and non-growing (November to March) seasons.

Prey Seasons	**WOLF WINTER**
Moose Winter	HABITAT x ELEVATION x SLOPE x ASPECT x WOLF RISK
Caribou Winter	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION x WOLF RISK
Sheep Early Winter	HABITAT x ELEVATION x SLOPE x ASPECT x CURVATURE x WOLF RISK
Elk Non-Growing Season	Non-Growing Season Feeding Habitat, November to March, as ranked in MKMA Conservation Area Design
	WOLF LATE WINTER
Moose Late Winter	HABITAT x ELEVATION x SLOPE x ASPECT x WOLF RISK
Caribou Spring	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION x WOLF RISK
Sheep Late Winter	HABITAT x ELEVATION x SLOPE x ASPECT x CURVATURE x WOLF RISK
Elk Non-Growing Season	Non-Growing Season Feeding Habitat, November to March, as ranked in MKMA Conservation Area Design
	WOLF DENNING
Moose Calving	HABITAT x ELEVATION x SLOPE x ASPECT x WOLF RISK x BEAR RISK x QUALITY
Caribou Calving	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION
Sheep Lambing	HABITAT x ELEVATION x SLOPE x CURVATURE x WOLF RISK x BEAR RISK x QUALITY
Elk Growing Season	Growing Season Feeding Habitat, April to October, as ranked in MKMA Conservation Area Design

Table B1 Continued

Prey Seasons	WOLF LATE SUMMER
Moose Summer	HABITAT x ELEVATION x SLOPE x ASPECT x WOLF RISK x BEAR RISK x BIOMASS x QUALITY
Caribou Summer	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION
Sheep Summer	HABITAT x ELEVATION x SLOPE x CURVATURE x WOLF RISK x BEAR RISK x QUALITY
Elk Growing Season	Growing Season Feeding Habitat, April to October, as ranked in MKMA Conservation Area Design
	WOLF FALL
Moose Rut	HABITAT x ELEVATION x SLOPE x ASPECT x BEAR RISK x BIOMASS
Caribou Rut	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION
Sheep Rut	HABITAT x ELEVATION x SLOPE x ASPECT x CURVATURE x WOLF RISK
Elk Non-Growing Season	Non-Growing Season Feeding Habitat, November to March, as ranked in MKMA Conservation Area Design

Table B2. Summary of all candidate models used in analyses of seasonal selection by wolves in the Besa-Prophet study area. 2001-2004. Seasons are: winter (1 January - 28 February), late winter (1 March - 31 April), denning (1 May - 31 July), late summer (1 August - 30 September), and fall (1 October - 31 December). Parameters representing habitat and landscape features are: H = habitat class, A = aspect, E = elevation (quadratic), S = slope (quadratic), F = fragmentation (habitat complexity), B = biomass (Denning, June NDVI; Late Summer, August NDVI), Q = quality (denning models, change in NDVI between June and July; late summer models, change in NDVI between August and September). Parameters representing relative selection value by prey are: M = moose, C = caribou, S = Stone's sheep, E = elk during seasons that most appropriately overlap with the wolf seasons.

Winter	Late Winter	Denning		Late Summer		Fall
H	H	H	B x S x F	H	B x S x F	H
H x A	H x A	H x A	B x S x F x A	H x A	B x S x F x A	H x A
H x E	H x E	H x E	Q	H x E	Q	H x E
H x F	H x F	H x F	Q x A	H x F	Q x A	H x F
H x E x A	H x E x A	H x E x A	Q x E	H x E x A	Q x E	H x E x A
H x E x F	H x E x F	H x E x F	Q x F	H x E x F	Q x F	H x E x F
H x F x A	H x F x A	H x F x A	Q x E x A	H x F x A	Q x E x A	H x F x A
H x E x F x A	H x E x F x A	H x E x F x A	Q x E x F	H x E x F x A	Q x E x F	H x E x F x A
H x S	H x S	H x S	Q x F x A	H x S	Q x F x A	H x S
H x S x A	H x S x A	H x S x A	Q x E x F x A	H x S x A	Q x E x F x A	H x S x A
H x S x F	H x S x F	H x S x F	Q x S	H x S x F	Q x S	H x S x F
H x S x F x A	H x S x F x A	H x S x F x A	Q x S x A	H x S x F x A	Q x S x A	H x S x F x A
		B	Q x S x F	B	Q x S x F	
		B x A	Q x S x F x A	B x A	Q x S x F x A	
		B x E	M	B x E	M	
		B x F	C	B x F	C	
		B x E x A	S	B x E x A	S	
		B x E x F	E	B x E x F	E	
		B x F x A	C x S	B x F x A	C x S	
		B x E x F x A	M x E	B x E x F x A	M x E	
		B x S	E x S	B x S	E x S	
		B x S x A	M x E x C x S	B x S x A	M x E x C x S	

Table B3. The top global models estimated to best represent the relative likelihood of occurrence of wolves in the Besa-Prophet study area in winter (1 January - 28 February), late winter (1 March - 31 April), denning (1 May - 31 July), late summer (1 August - 30 September), and fall (1 October - 31 December), pooled across 2001 to 2004.

Pack	Season	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]
All Wolves	Winter	H x E x F x A	18	0.00	0.99	0.87
All Wolves	Late Winter	H x E x F x A	18	0.00	0.99	0.91
All Wolves	Denning	H x S x F x A	18	0.00	0.99	0.98
All Wolves	Late Summer	H x S x F x A	18	0.00	0.77	0.97
		H x S x A	16	2.43	0.23	0.98
All Wolves	Fall	H x S x F x A	18	0.00	0.82	0.99
		H x S x A	16	3.02	0.18	0.98

[a] Explanatory variables in the pooled models for all wolves included habitat class (H), elevation (E), fragmentation (F), aspect (A), slope (S).
[b] Number of model parameters.
[c] Difference in Akaike's Information Criteria (adjusted for small sample sizes) values between the best fitting model and model *i*.
[d] Akaike weights, scaled 0 – 1, indicate the degree of relative support for each model.
[e] Spearman's rank correlation coefficient; values > 0.70 indicate good model performance.

Table B4. The top models estimated to best represent areas with highest selection value by wolf packs in the Besa-Prophet study area in winter (1 January - 28 February), late winter (1 March - 31 April), denning (1 May - 31 July), late summer (1 August - 30 September), and fall (1 October - 31 December), pooled across 2001 to 2004 (unless otherwise indicated).

Pack	Season	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]
Pocketknife	Winter	H x E x F x A	16	0.00	0.74	0.67
		H x S x F x A	16	3.51	0.13	0.70
		H x F x A	14	4.43	0.08	0.52
	Late Winter	H x E x A	14	0.00	0.52	0.85
		H x E x F x A	16	0.25	0.46	0.81
	Denning	B x S x A	8	0.00	0.76	0.83
		B x S x F x A	10	2.32	0.24	0.80
	Late Summer (02)	H x E x F	11	0.00	0.92	0.80
	Fall (02)	H x S x F	14	0.00	0.55	0.75
		H x S x F x A	18	0.93	0.34	0.77
		H x S	12	3.93	0.08	0.23
Lower Besa	Winter	H x E	11	0.00	0.57	0.61
		H x E x F	13	2.58	0.16	0.73
		H	9	4.09	0.07	0.25
		H x E x A	15	4.59	0.06	0.73
		H x S	11	4.74	0.05	0.60
		H x F	11	6.29	0.02	0.36
	Late Winter	H x E x F x A	17	0.00	0.99	0.72
	Denning	B x S x F x A	10	0.00	1.00	0.89
	Late Summer	B x S x F	6	0.00	0.48	0.88
		H x E x F x A	18	0.81	0.32	0.82
		H x E x A	16	3.50	0.08	0.89
		B x S x F x A	10	4.45	0.05	0.91
		B x S	4	4.82	0.04	0.88
	Fall	H x S	12	0.00	0.62	0.72
		H x S x A	16	1.81	0.25	0.65
		H x S x F	14	3.82	0.09	0.78
Dopp	Late Winter (02)	H x E x F x A	18	0.00	0.92	0.91
	Denning (02)	H x E x A	16	0.00	0.75	0.91
		H x E x F x A	18	3.22	0.15	0.91
		H x S x A	16	5.21	0.06	0.93
	Late Summer (02)	H x S	11	0.00	0.60	0.85
		H x S x A	15	1.66	0.26	0.82
		H x S x F	13	3.79	0.09	0.81
	Fall (02)	H x E	12	0.00	0.66	0.88
		H x E x F	14	1.69	0.28	0.84

Table B4 Continued

Pack	Season	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]
Keily	Winter (03)	H x E	12	0.00	0.38	0.71
		H x E x A	16	0.86	0.25	0.71
		H x E x F	14	2.55	0.11	0.75
		H x E x F x A	18	3.19	0.08	0.66
		H x S x A	16	3.24	0.08	0.74
		H x S x Fx A	18	4.34	0.04	0.71
	Late Winter (03)	H x E x A	16	0.00	0.56	0.86
		H x E x F x A	18	0.46	0.44	0.76
	Denning (03)	H x S x Fx A	18	0.00	0.66	0.85
		H x S x A	16	2.89	0.16	0.85
		B x S x F x A	10	2.98	0.15	0.90
Richards	Late Winter (02)	H x E x A	16	0.00	0.75	0.90
		H x E x F x A	18	2.27	0.24	0.92
	Denning (02)	H x S x A	16	0.00	0.53	0.93
		H x S x F x A	18	2.47	0.16	0.88
		P: M x E x C x S	5	3.47	0.09	0.83
		H x S	12	3.54	0.09	0.94
		P: M x E	5	3.56	0.09	0.80
	Late Summer (02)	H x S	12	0.00	0.83	0.82
		H x S x F	14	4.09	0.11	0.85
		H x S x A	16	7.07	0.02	0.80
	Fall (02)	M x E x C x S	5	0.00	0.54	0.87
		M x E	3	0.30	0.46	0.90
Prophet	Winter	H x E x F	14	0.00	0.60	0.90
		H x E x F x A	18	0.85	0.39	0.87
	Late Winter	H x E x A	16	0.00	0.81	0.96
		H x E x F x A	18	2.96	0.18	0.76
	Denning	H x E x F	14	0.00	0.58	0.92
		H x E	12	1.60	0.26	0.93
		H x E x F x A	18	3.42	0.11	0.94
	Fall (03)	H x S x F	14	0.00	0.89	0.89
		H x S x F x A	18	4.88	0.08	0.93

Table B4 Continued

Pack	Season	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]
Nevis	Winter	H x E	12	0.00	0.61	0.70
		H x E x F	14	2.10	0.21	0.72
		H x E x A	16	3.11	0.13	0.56
	Late Winter	H x E x A	16	0.00	0.44	0.76
		H x E	12	0.51	0.34	0.70
		H x E x F x A	18	2.36	0.13	0.64
		H x E x F	14	3.15	0.09	0.82
	Denning	H x S x A	16	0.00	0.68	0.88
		H x S x F x A	18	1.65	0.30	0.87
	Late Summer	H x S x F x A	18	0.00	0.68	0.89
		H x S x A	16	1.49	0.32	0.84
	Fall	H x S x F x A	18	0.00	0.88	0.87
		H x S x A	16	4.65	0.09	0.84

[a] Explanatory variables in the pooled models for individual wolf packs included habitat class (H), elevation (E), fragmentation (F), aspect (A), slope (S), habitat biomass as determined by absolute NDVI (B), habitat quality as determined by change in NDVI (Q), an interaction between habitat biomass and quality (BQ), and a GIS layer indicative of the relative selection value for prey (P: M(moose) E(elk) C(caribou) S(sheep).
[b] Number of model parameters.
[c] Difference in Akaike's Information Criteria (adjusted for small sample sizes) values between the best fitting model and model *i*.
[d] Akaike weights, scaled 0 – 1, indicate the degree of relative support for each model.
[e] Spearman's rank correlation coefficient; values > 0.70 indicate good model performance.

Appendix C: Final rankings and performance of models used to evaluate selection of resources by grizzly bears in the Besa-Prophet area of northern British Columbia. Models were developed across three seasons and from 1-4 years (2001-2004).

Table C1. Seasonal models used in developing surfaces of selection value for potential prey species of grizzly bears in the Besa-Prophet study area, 2001 - 2004. Grizzly bear seasons were paired with the closest corresponding prey seasons for moose (Gillingham and Parker 2008a), woodland caribou (Gustine 2005), and Stone's sheep (Walker 2005). Habitat classes were grouped slightly differently in models for each species. Wolf risk and bear risk are measures of the relative risk of predation from wolves and grizzly bears from a prey perspective. Biomass and quality are indices of vegetation quantity (NDVI) and quality (change in NDVI). Curvature is an overall index of the concavity or convexity of a sampled pixel. Elevation was entered as a quadratic function. Elk layers were obtained from the Conservation Area Design for the Muskwa-Kechika Management Area (Heinemeyer et al. 2004a, b) during the growing season (April through October).

GRIZZLY BEAR SPRING	
Prey Seasons	
Moose Calving	HABITAT x ELEVATION x SLOPE x ASPECT x WOLF RISK x BEAR RISK x QUALITY
Caribou Calving	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION
Sheep Lambing	HABITAT x ELEVATION x SLOPE x CURVATURE x WOLF RISK x BEAR RISK x QUALITY
Elk Growing Season	Growing Season Feeding Habitat, April to October, as ranked in MKMA Conservation Area Design

GRIZZLY BEAR SUMMER	
Prey Seasons	
Moose Summer	HABITAT x ELEVATION x SLOPE x ASPECT x WOLF RISK x BEAR RISK x BIOMASS x QUALITY
Caribou Summer	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION
Sheep Summer	HABITAT x ELEVATION x SLOPE x CURVATURE x WOLF RISK x BEAR RISK x QUALITY
Elk Growing Season	Growing Season Feeding Habitat, April to October, as ranked in MKMA Conservation Area Design

GRIZZLY BEAR FALL	
Prey Seasons	
Moose Rut	HABITAT x ELEVATION x SLOPE x ASPECT x BEAR RISK x BIOMASS
Caribou Fall	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION
Sheep Fall	HABITAT x ELEVATION x CURVATURE x WOLF RISK x BEAR RISK
Elk Growing Season	Growing Season Feeding Habitat, April to October, as ranked in MKMA Conservation Area Design

Table C2. Summary of all candidate models used in analyses of seasonal selection by female grizzly bears in the Besa-Prophet study area, 2001-2004. Seasons are: spring (den emergence to June 15), summer (June 16 to August 15), and fall (August 16 to denning). Parameters representing habitat and landscape features are: H = habitat class, A = aspect, E = elevation (quadratic), S = slope (quadratic), F = fragmentation (habitat complexity), B = biomass (Spring, June NDVI; Summer, July NDVI; Fall, September NDVI), Q = quality (summer models; change in NDVI between June and July). Parameters representing relative selection value by prey are: M = moose, C = caribou, S = Stone's sheep, E = elk during seasons that most appropriately overlap with the bear seasons.

Spring	Summer		Fall
H	H	Q x S	H
H x A	H x A	Q x S x A	H x A
H x E	H x E	Q x S x F	H x E
H x F	H x F	Q x S x F x A	H x F
H x E x A	H x E x A	M	H x E x A
H x E x F	H x E x F	C	H x E x F
H x F x A	H x F x A	S	H x F x A
H x E x F x A	H x E x F x A	E	H x E x F x A
H x S	H x S	C x S	H x S
H x S x A	H x S x A	M x E	H x S x A
H x S x F	H x S x F	E x S	H x S x F
H x S x F x A	H x S x F x A	M x E x C x S	H x S x F x A
B	B		B
B x A	B x A		B x A
B x E	B x E		B x E
B x F	B x F		B x F
B x E x A	B x E x A		B x E x A
B x E x F	B x E x F		B x E x F
B x F x A	B x F x A		B x F x A
B x E x F x A	B x E x F x A		B x E x F x A
B x S	B x S		B x S
B x S x A	B x S x A		B x S x A
B x S x F	B x S x F		B x S x F
B x S x F x A	B x S x F x A		B x S x F x A
M	Q		M
C	Q x A		C
S	Q x E		S
E	Q x F		E
C x S	Q x E x A		C x S
M x E	Q x E x F		M x E
E x S	Q x F x A		E x S
M x E x C x S	Q x E x F x A		M x E x C x S

Table C1. Seasonal models used in developing surfaces of selection value for potential prey species of grizzly bears in the Besa-Prophet study area, 2001 - 2004. Grizzly bear seasons were paired with the closest corresponding prey seasons for moose (Gillingham and Parker 2008a), woodland caribou (Gustine 2005), and Stone's sheep (Walker 2005). Habitat classes were grouped slightly differently in models for each species. Wolf risk and bear risk are measures of the relative risk of predation from wolves and grizzly bears from a prey perspective. Biomass and quality are indices of vegetation quantity (NDVI) and quality (change in NDVI). Curvature is an overall index of the concavity or convexity of a sampled pixel. Elevation was entered as a quadratic function. Elk layers were obtained from the Conservation Area Design for the Muskwa-Kechika Management Area (Heinemeyer et al. 2004a, b) during the growing season (April through October).

GRIZZLY BEAR SPRING	
Prey Seasons	
Moose Calving	HABITAT x ELEVATION x SLOPE x ASPECT x WOLF RISK x BEAR RISK x QUALITY
Caribou Calving	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION
Sheep Lambing	HABITAT x ELEVATION x SLOPE x CURVATURE x WOLF RISK x BEAR RISK x QUALITY
Elk Growing Season	Growing Season Feeding Habitat, April to October, as ranked in MKMA Conservation Area Design

GRIZZLY BEAR SUMMER	
Prey Seasons	
Moose Summer	HABITAT x ELEVATION x SLOPE x ASPECT x WOLF RISK x BEAR RISK x BIOMASS x QUALITY
Caribou Summer	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION
Sheep Summer	HABITAT x ELEVATION x SLOPE x CURVATURE x WOLF RISK x BEAR RISK x QUALITY
Elk Growing Season	Growing Season Feeding Habitat, April to October, as ranked in MKMA Conservation Area Design

GRIZZLY BEAR FALL	
Prey Seasons	
Moose Rut	HABITAT x ELEVATION x SLOPE x ASPECT x BEAR RISK x BIOMASS
Caribou Fall	HABITAT x ELEVATION x SLOPE x ASPECT x FRAGMENTATION
Sheep Fall	HABITAT x ELEVATION x CURVATURE x WOLF RISK x BEAR RISK
Elk Growing Season	Growing Season Feeding Habitat, April to October, as ranked in MKMA Conservation Area Design

Table C3. The top global models describing seasonal habitat selection by female grizzly bears in the Besa-Prophet study area of northern British Columbia by year and pooled across years (2001-2004).

Spring					Summer					Fall				
Model[a]	**K[b]**	**Δ_i[c]**	**w_i[d]**	**r_s[e]**	**Model[a]**	**K[b]**	**Δ_i[c]**	**w_i[d]**	**r_s[e]**	**Model[a]**	**K[b]**	**Δ_i[c]**	**w_i[d]**	**r_s[e]**
2001					2001					2001				
HEFA	18	0.00	0.75	0.94	HEA	16	0.00	0.85	0.94	HEFA	18	0.00	0.99	0.97
BEFA	10	3.17	0.15	0.95	HEFA	18	3.48	0.15	0.93					
HEF	14	4.05	0.10	0.94										
2002					2002					2002				
HSA	16	0.00	0.8	0.87	HEFA	18	0.00	0.99	0.99	HEA	16	0.00	0.79	0.97
HSFA	18	3.49	0.14	0.80						HEFA	18	3.26	0.16	0.97
HS	12	5.69	0.05	0.79						HE	12	5.8	0.04	0.97
2003					2003					2003				
HEFA	18	0.00	1	0.95	HEFA	18	0.00	0.98	0.97	HEFA	18	0.00	0.98	0.98
2004					2004					2004				
HSFA	18	0.00	1	0.87	HSFA	18	0.00	0.69	0.90	HEFA	18	0.00	0.97	0.91
					QEFA	10	1.86	0.27	0.92					
Pooled					Pooled					Pooled				
HEFA	18	0.00	1	0.99	HEFA	18	0.00	1.00	0.99	HEFA	18	0.00	1.00	0.99

[a] Explanatory variables in the global models include habitat class (H), elevation (E), fragmentation (F), aspect (A), slope (S), habitat biomass as determined by absolute NDVI (B), habitat quality as determined by change in NDVI (Q).
[b] Number of model parameters.
[c] Difference in Akaike's Information Criteria (adjusted for small sample sizes) between the best fitting model and model *i*.
[d] Akaike weights, scaled 0 – 1, indicate the degree of relative support for each model.
[e] Spearman's rank correlation coefficient (reflective of model predictability).

Table C3. The top global models describing seasonal habitat selection by female grizzly bears in the Besa-Prophet study area of northern British Columbia by year and pooled across years (2001-2004).

Spring					Summer					Fall				
Model[a]	**K[b]**	**Δ_i[c]**	**w_i[d]**	**r_s[e]**	**Model[a]**	**K[b]**	**Δ_i[c]**	**w_i[d]**	**r_s[e]**	**Model[a]**	**K[b]**	**Δ_i[c]**	**w_i[d]**	**r_s[e]**
2001					2001					2001				
HEFA	18	0.00	0.75	0.94	HEA	16	0.00	0.85	0.94	HEFA	18	0.00	0.99	0.97
BEFA	10	3.17	0.15	0.95	HEFA	18	3.48	0.15	0.93					
HEF	14	4.05	0.10	0.94										
2002					2002					2002				
HSA	16	0.00	0.8	0.87	HEFA	18	0.00	0.99	0.99	HEA	16	0.00	0.79	0.97
HSFA	18	3.49	0.14	0.80						HEFA	18	3.26	0.16	0.97
HS	12	5.69	0.05	0.79						HE	12	5.8	0.04	0.97
2003					2003					2003				
HEFA	18	0.00	1	0.95	HEFA	18	0.00	0.98	0.97	HEFA	18	0.00	0.98	0.98
2004					2004					2004				
HSFA	18	0.00	1	0.87	HSFA	18	0.00	0.69	0.90	HEFA	18	0.00	0.97	0.91
					QEFA	10	1.86	0.27	0.92					
Pooled					Pooled					Pooled				
HEFA	18	0.00	1	0.99	HEFA	18	0.00	1.00	0.99	HEFA	18	0.00	1.00	0.99

[a] Explanatory variables in the global models include habitat class (H), elevation (E), fragmentation (F), aspect (A), slope (S), habitat biomass as determined by absolute NDVI (B), habitat quality as determined by change in NDVI (Q).
[b] Number of model parameters.
[c] Difference in Akaike's Information Criteria (adjusted for small sample sizes) between the best fitting model and model *i*.
[d] Akaike weights, scaled 0 – 1, indicate the degree of relative support for each model.
[e] Spearman's rank correlation coefficient (reflective of model predictability).

Table C4. The top models describing seasonal habitat selection by individual female grizzly bears in the Besa-Prophet area of northern British Columbia pooled across years (2001-2004).

Bear	Spring					Summer					Fall				
	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]
G01	H S F A	16	0.00	0.41	0.86	H S F A	18	0.00	0.71	0.84	H E F A	18	0.00	0.87	0.94
	H S A	14	0.57	0.31	0.85	H S A	16	1.82	0.29	0.85	H E F	14	4.56	0.09	0.93
	H E FA	16	1.70	0.18	0.85										
	B S A	7	4.27	0.05	0.88										
G05	H S F A	17	0.00	0.66	0.94	H S F A	18	0.00	0.80	0.89	H E F A	18	0.00	0.75	0.91
	H S A	15	1.36	0.34	0.94	H E F A	18	3.62	0.13	0.92	H E A	16	2.20	0.25	0.89
						H S A	16	5.44	0.05	0.90					
G08	H E FA	18	0.00	0.68	0.92	H E A	16	0.00	0.66	0.94	H E F A	18	0.00	0.81	0.91
	H E F	14	2.95	0.16	0.92	H E F A	18	1.46	0.32	0.95	H E F	14	3.01	0.18	0.93
	B E F A	10	3.38	0.13	0.92										
G15	H E	12	0.00	0.40	0.80	H E A	16	0.00	0.61	0.80	H S F A	18	0.00	0.59	0.83
	B E	4	1.75	0.17	0.67	H E F A	18	2.23	0.20	0.72	H S F	14	0.81	0.39	0.83
	B S	4	2.22	0.13	0.7	H A	14	3.45	0.11	0.55					
	B S A	8	3.49	0.07	0.66	H F A	16	5.22	0.04	0.69					
	H E F	14	3.77	0.06	0.71										
	H E A	16	4.46	0.04	0.63										
	B E A	8	4.66	0.04	0.61										
	B E F	6	5.29	0.03	0.63										
	B S F	6	5.79	0.02	0.68										
G18	H E FA	18	0.00	0.74	0.81	H S F A	18	0.00	0.68	0.86	H E F A	18	0.00	0.89	0.94
	B E F A	10	2.23	0.24	0.83	H S A	16	1.51	0.32	0.89	H E A	16	4.41	0.10	0.95

Table C4. Continued

Bear	Spring					Summer					Fall				
	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]
G20	H S A	16	0.00	0.34	0.67	H A	14	0.00	0.43	0.49	H E	12	0.00	0.69	0.70
	H S	12	0.43	0.27	0.52	H S A	16	1.34	0.22	0.72	H E F	14	2.89	0.16	0.68
	B S A	8	0.96	0.21	0.82	H E A	16	2.67	0.11	0.76	H E A	16	4.66	0.07	0.79
	H S F A	18	3.50	0.06	0.55	H F A	16	2.69	0.11	0.70	P: M E C S	5	5.95	0.04	0.72
	B S F A	10	3.88	0.05	0.56	H S F A	18	4.04	0.06	0.73					
	H S F	14	4.01	0.05	0.56	H E F A	18	5.45	0.03	0.71					
G21	B E A	7	0.00	0.82	0.71	H E F	14	0.00	0.92	0.88	H E F A	18	0.00	0.74	0.95
	B E F A	9	3.11	0.17	0.71						H E F	14	2.15	0.25	0.95
G22	H S F A	15	0.00	0.98	0.77	H S F A	18	0.00	0.59	0.92	H E A	16	0.00	0.60	0.91
						H S A	16	1.21	0.32	0.89	H E F A	18	2.27	0.19	0.83
						H E A	16	5.05	0.05	0.94	H E	12	3.56	0.10	0.88
											H E F	14	5.60	0.04	0.83
											H S A	16	6.18	0.03	0.88
G23	B E F A	9	0.00	0.68	0.77	H E A	16	0.00	0.74	0.90	H E A	15	0.00	0.84	0.78
	H E FA	17	2.79	0.17	0.83	H E F A	18	4.04	0.10	0.89	H E F A	17	3.38	0.15	0.79
	H E A	15	4.69	0.07	0.77	(BQ) E A	8	4.54	0.08	0.90					
	B E A	7	5.74	0.04	0.77	H E	12	6.09	0.04	0.85					
G24	H E F	13	0.00	0.76	0.73	H S A	15	0.00	0.63	0.80	H S F A	18	0.00	0.35	0.82
	H E FA	16	2.91	0.18	0.80	H S F A	17	1.10	0.37	0.82	H E A	16	0.20	0.32	0.80
	H E	11	5.84	0.04	0.74						H E F A	18	0.57	0.26	0.81
											H S A	16	3.31	0.07	0.62

Table C4. Continued

Bear	Spring					Summer					Fall				
	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]	Model[a]	K[b]	Δ_i[c]	w_i[d]	r_s[e]
G25	H S F A	17	0.00	1.00	0.78	H S F A	18	0.00	0.47	0.95	H E A	16	0.00	0.52	0.82
						H F A	16	0.17	0.44	0.92	H E	12	1.17	0.29	0.85
						H E F A	18	3.33	0.09	0.94	H E F A	18	2.97	0.12	0.80
											H E F	14	4.20	0.06	0.85
G26	H S F A	18	0.00	0.63	0.90	H E F A	18	0.00	0.69	0.93	H S F	14	0.00	0.92	0.91
	H S A	16	1.10	0.36	0.83	H S F A	18	2.64	0.19	0.90					
						H E A	16	5.27	0.05	0.90					
						H S A	16	5.32	0.05	0.80					
G27	H S F	18	0.00	0.99	0.76	Q E F	6	0.00	0.42	0.81	H S A	14	0.00	0.43	0.84
						P: M E C S	5	0.81	0.28	0.77	H E A	14	1.72	0.18	0.87
						Q E	4	2.28	0.14	0.79	H S F A	16	1.99	0.16	0.85
						Q E F A	10	2.96	0.10	0.79	H A	12	2.65	0.11	0.44
						Q E A	8	5.07	0.03	0.80	H E F A	16	4.22	0.05	0.87

[a] Explanatory variables in the pooled models include habitat class (H), elevation (E), fragmentation (F), aspect (A), slope (S), vegetation biomass as determined by absolute NDVI (B), vegetation quality as determined by change in NDVI (Q), an interaction between vegetation biomass and quality (BQ), and a GIS layer indicative of relative selection value for prey species (P: M(moose) E(elk) C(caribou) S(sheep).

[b] Number of model parameters.

[c] Difference in Akaike's Information Criteria (adjusted for small sample sizes) between the best fitting model and model *i*.

[d] Akaike weights, scaled 0 – 1, indicate the degree of relative support for each model.

[e] Spearman's rank correlation coefficient; values > 0.70 indicate good model performance.

Appendix D: Selection coefficients (β_i) and standard errors (SE) of attributes from final models that describe resource selection by grizzly bear family units.

Differences in movements and habitat selection between sexes or family units may be in response to resource competition or avoidance of energetically costly aggressive encounters (sic. Maraj 2007). Larger individuals or individuals not caring for young are able to occupy the best habitats (Berger 1991). Weaker or encumbered individuals – females with young or subadults – might maximize energy gains by selecting for the best habitats with the lowest probability of encountering dominant individuals (Ben David et al. 2004). In addition, because male grizzly bears sometimes kill and eat dependent cubs (McLellan 2005), movements and selection patterns of females with young may be related to avoidance of males.

In the BP, seasonal home ranges and movement rates of grizzly bears were a function of family status. I found that sizes of spring home ranges, as well as spring and summer movement rates, of sows with cubs-of-the-year (COY) were significantly less than those of other bear family groups. As a result of these differences, I examined whether habitat selection patterns also varied by family group. I pooled female grizzly bears across years according to family status (lone females, females with COY, females with yearlings, and females with juveniles (2-year olds). I followed the same procedures to model habitat selection as outlined in Chapter 4. Final selection coefficients are presented in Table D1. Females with yearlings showed the strongest patterns of selection, whereas females with cubs appeared to respond most directly to elevation and slope during spring. During the fall COY families selected shrub habitats and regenerating burns, while avoiding open alpine and non-vegetated areas. Yearling families tended to avoid conifer and open alpine habitats year round, as well as shrub habitats during the spring. Regenerating disturbed areas were

selected by yearling families year round, and shrub communities were selected during the summer and fall.

The predator avoidance hypothesis (e.g., Bleich et al. 1997) predicts that females will inhabit areas with more rugged terrain and/or a lower probability of encountering conspecifics. I was unable to map the distribution of males in the BP. However, the importance of elevation and slope to COY families in the BP may be partially in response to security requirements associated with the limited mobility of cubs. As cubs mature and become more agile, nutritional requirements may become more influential on habitat selection than avoidance of conspecifics. Family groups in Kluane National Park, Yukon, used significantly more rugged habitat than other cohorts, and terrain ruggedness was the primary habitat selection variable throughout the active period (Maraj 2007). In addition, the probability of a family group in Kluane encountering a conspecific was lower than for other cohorts, earlier in the growing season, and throughout the active period, forage productivity variables were more influential on habitat selection than were conspecific distributions. Given distinctive use of rugged areas by family groups but not by other cohorts, these areas were probably used primarily as security habitat for raising cubs (e.g., Pearson 1975; Stemlock 1981; Darling 1987). Maraj's study concluded that family groups may manifest avoidance by selecting for landscape features that females learned through experience provide security.

Appendix E: Den site characteristics for grizzly bears and wolves in the Besa-Prophet area of northern British Columbia.

Table E1. Characteristics of den sites used by individual grizzly bears in the Besa-Prophet area. Habitat classes are defined in Table 4.1.

Bear	Year	Habitat Class	Slope (°)	Elevation (m)	Aspect
G01	2001	*Elymus* burn	33	1365	E
	2002	Riparian	33	1302	S
	2003	Deciduous burn	36	1436	E
	2004	*Elymus* burn	41	1326	E
G05	2001	*Elymus* burn	32	1543	S
	2002	Non-vegetated	32	1374	W
	2003	Open alpine	41	1754	S
G08	2001	Alpine shrub	24	1721	S
	2002	Alpine shrub	30	1715	E
	2003	Riparian	22	1343	NE
	2004	Conifer	26	1545	NW
G15	2003	Conifer	26	1527	E
	2004	Alpine shrub	20	1742	E
G18	2001	Stunted spruce	46	1643	W
	2003	*Elymus* burns	27	1666	S
G20	2002	Stunted spruce	19	1172	S
	2003	Non-vegetated	28	1696	E
G21	2002	Non-vegetated	24	1784	E
	2003	Non-vegetated	35	1766	S
G22	2002	Open alpine	26	1882	E
G23	2002	Open alpine	29	1896	S
G24	2002	Open alpine	16	1793	S
	2003	Non-vegetated	31	1660	S
G25	2002	Non-vegetated	40	1870	S
	2003	Non-vegetated	38	1816	S
G26	2003	Non-vegetated	41	1965	W
G27	2003	Deciduous burn	31	1315	S

Table E2. Characteristics of den sites used by wolf packs in the Besa-Prophet area. Habitat classes are defined in Table 3.1.

Pack	Year	Habitat Class	Slope (°)	Elevation (m)	Aspect
Pocketknife	2002	Riparian spruce	3	1040	E
	2003	Riparian spruce	3	1040	E
Lower Besa	2002	Riparian spruce	2	948	S
	2003	Riparian spruce	2	868	W
Dopp	2002	Conifer	16	1315	S
Keily	2003	Conifer	19	1406	S
Richards	2002	Riparian spruce	4	1259	S
Prophet	2003	Conifer	25	1398	E
	2004	Conifer	20	1474	S
Nevis	2002	Shrub	7	1268	N
	2003	Shrub	4	1274	S
	2004	Riparian spruce	4	1386	S

Table 3.4. Resource selection coefficients (± SE) representing seasonal selection patterns across wolves (global) and by wolf pack for habitat classes (as described in Table 3.1) in the Besa-Prophet study area of northern British Columbia. Coefficients are based on pooled data between 2001 and 2004. Values in bold indicate significant selection (positive values) or avoidance (negative values) as determined by 95 % confidence intervals. Blanks indicate those variables/parameters that were not included in final model rankings or could not be tested because of zero use.

PACK	Season [a]	Conifer	Stunted Spruce	Shrub	Alpine Shrub	Non-Vegetated	Riparian Spruce	Open Alpine	Deciduous Burns	*Elymus* Burns	Sub-Alpine Spruce
GLOBAL	**Winter**	**-0.86 ± 0.10**	**-0.46 ± 0.16**	**1.13 ± 0.10**	0.19 ± 0.16	**-0.59 ± 0.16**	-0.13 ± 0.11	**0.47 ± 0.17**	**-0.34 ± 0.14**	**0.53 ± 0.16**	0.07 ± 0.16
	L. Winter	**-0.73 ± 0.07**	**-0.27 ± 0.10**	**0.34 ± 0.08**	-0.06 ± 0.15	-0.20 ± 0.10	**0.19 ± 0.08**	**0.52 ± 0.15**	0.03 ± 0.09	**0.67 ± 0.10**	**-0.48 ± 0.15**
	Denning	**-0.35 ± 0.06**	**-0.25 ± 0.12**	**0.70 ± 0.07**	**0.37 ± 0.08**	**-0.67 ± 0.11**	0.06 ± 0.07	**-0.51 ± 0.11**	-0.03 ± 0.11	**0.75 ± 0.14**	-0.06 ± 0.12
	L. Summer	**-0.39 ± 0.10**	-0.29 ± 0.19	**0.70 ± 0.11**	**0.97 ± 0.11**	**-1.28 ± 0.21**	-0.03 ± 0.11	**0.34 ± 0.13**	-0.11 ± 0.17	-0.34 ± 0.35	**0.43 ± 0.17**
	Fall	**-0.68 ± 0.08**	**-0.59 ± 0.16**	**0.79 ± 0.09**	**0.53 ± 0.08**	**-0.76 ± 0.12**	**-0.35 ± 0.09**	0.09 ± 0.10	**0.37 ± 0.11**	0.31 ± 0.17	**0.30 ± 0.12**
POCKET-KNIFE	**Winter**	**-0.76 ± 0.26**	-0.47 ± 0.34	**1.04 ± 0.25**		-1.36 ± 0.90	-0.09 ± 0.25	0.83 ± 0.54	-0.34 ± 0.33	**1.14 ± 0.37**	
	L. Winter	**-0.91 ± 0.21**	**-0.74 ± 0.33**	**1.17 ± 0.21**		0.08 ± 0.43	0.40 ± 0.21	0.68 ± 0.55	**-0.71 ± 0.32**	0.03 ± 0.36	
	Denning [b]										
	L. Summer	**-1.96 ± 0.34**	**-1.81 ± 0.43**	0.09 ± 0.32	**4.44 ± 0.85**		-0.57 ± 0.32	**2.09 ± 0.61**	**-2.29 ± 0.52**		
	Fall	**-0.86 ± 0.29**	-0.81 ± 0.54	-0.01 ± 0.34	-0.63 ± 0.98	-0.65 ± 0.81	-0.79 ± 0.30	**1.73 ± 0.38**	0.24 ± 0.37	0.84 ± 0.70	0.94 ± 0.72
LOWER-BESA	**Winter**	-0.48 ± 0.32	0.13 ± 0.33	**1.12 ± 0.32**	0.003 ± 0.99	-0.15 ± 0.48	0.49 ± 0.32	-0.91 ± 0.96	-0.30 ± 0.35	0.10 ± 0.44	
	L. Winter	**-1.07 ± 0.23**	**-0.93 ± 0.29**	0.19 ± 0.27	1.45 ± 0.84	-0.13 ± 0.32	-0.10 ± 0.24	0.53 ± 0.64	-0.24 ± 0.23	0.31 ± 0.27	
	Denning [b]										
	L. Summer	-0.28 ± 0.30	-0.45 ± 0.38	0.11 ± 0.28	1.05 ± 1.13	-0.54 ± 0.53	0.09 ± 0.25	0.77 ± 0.77	-0.40 ± 0.38	-0.82 ± 0.74	0.47 ± 0.69
	Fall	-0.19 ± 0.21	-0.32 ± 0.28	**1.13 ± 0.24**	0.11 ± 0.58	-0.02 ± 0.42	-0.30 ± 0.25	-0.34 ± 0.51	**0.57 ± 0.22**	-0.52 ± 0.51	-0.11 ± 0.50
DOPP	**L. Winter**	-0.21 ± 0.21	0.22 ± 0.34	**-1.22 ± 0.45**	0.03 ± 0.32	0.008 ± 0.29	0.13 ± 0.26	0.61 ± 0.41	**0.77 ± 0.26**	**1.09 ± 0.46**	**-1.41 ± 0.49**
	Denning	-0.28 ± 0.19	**-1.27 ± 0.56**	-0.39 ± 0.37	**0.84 ± 0.26**	-0.35 ± 0.29	0.14 ± 0.25	**0.75 ± 0.35**	-0.42 ± 0.30	0.53 ± 0.41	0.45 ± 0.29
	L. Summer	-0.03 ± 0.27		0.35 ± 0.44	**1.38 ± 0.26**	**-2.06 ± 0.52**	0.03 ± 0.35	**0.67 ± 0.33**	-0.79 ± 0.71	-0.21 ± 0.97	0.66 ± 0.37
	Fall	**-0.64 ± 0.24**	-1.19 ± 0.61	0.43 ± 0.30	**1.43 ± 0.40**	-0.66 ± 0.37	-0.51 ± 0.35	**1.44 ± 0.55**	-0.60 ± 0.41	-0.20 ± 0.60	0.50 ± 0.31
KEILY	**Winter**	**-0.96 ± 0.34**	-0.59 ± 0.57	0.31 ± 0.55	**0.96 ± 0.40**	-0.23 ± 0.47	-0.47 ± 0.55	**1.23 ± 0.50**	-1.37 ± 0.75	0.30 ± 0.55	0.81 ± 0.42
	L. Winter	-0.05 ± 0.15	-0.35 ± 0.25	**-0.51 ± 0.24**	-0.19 ± 0.25	-0.25 ± 0.22	0.11 ± 0.19	0.58 ± 0.34	**0.74 ± 0.18**	0.46 ± 0.27	**-0.55 ± 0.27**
	Denning	**0.40 ± 0.16**	0.26 ± 0.29	0.04 ± 0.33	0.31 ± 0.18	-0.66 ± 0.35	0.41 ± 0.26	**-0.76 ± 0.34**	0.32 ± 0.32	-0.54 ± 0.59	0.22 ± 0.28
RICHARDS	**L. Winter**	**-0.86 ± 0.33**	0.18 ± 0.39	0.18 ± 0.34	-0.03 ± 0.72	-0.36 ± 0.45	-0.005 ± 0.38	1.30 ± 0.78	-0.17 ± 0.43	0.67 ± 0.45	-0.91 ± 0.93
	Denning	**-0.33 ± 0.16**	-0.12 ± 0.28	**0.44 ± 0.22**	-0.18 ± 0.17	**-0.96 ± 0.26**	**0.67 ± 0.22**	**-0.48 ± 0.23**	0.27 ± 0.30	**0.63 ± 0.30**	0.07 ± 0.22
	L. Summer	-0.13 ± 0.30	-1.28 ± 0.93	**0.92 ± 0.36**	0.15 ± 0.32	-0.79 ± 0.40	**0.92 ± 0.37**	**-1.02 ± 0.48**	0.06 ± 0.58	1.03 ± 0.81	0.14 ± 0.39
	Fall [c]										
PROPHET	**Winter**	**-0.58 ± 0.22**	-0.05 ± 0.36	**1.22 ± 0.26**	-0.37 ± 0.34	**-0.69 ± 0.27**	-0.01 ± 0.28	-0.23 ± 0.42	-0.08 ± 0.35	**1.00 ± 0.31**	-0.22 ± 0.30
	L. Winter	**-0.75 ± 0.23**	-0.50 ± 0.37	-0.04 ± 0.24	0.26 ± 0.36	-0.22 ± 0.21	0.29 ± 0.22	0.37 ± 0.45	0.36 ± 0.31	**0.91 ± 0.31**	-0.67 ± 0.40
	Denning	**-0.76 ± 0.20**	**-1.41 ± 0.43**	**0.82 ± 0.20**	**1.04 ± 0.19**	**-0.60 ± 0.22**	0.29 ± 0.23	**0.62 ± 0.28**	0.11 ± 0.28	0.28 ± 0.25	-0.38 ± 0.28
	Fall	-0.13 ± 0.28	-1.29 ± 1.02	0.35 ± 0.32	**0.85 ± 0.22**	**-1.02 ± 0.40**	-0.24 ± 0.33	-0.49 ± 0.33	0.71 ± 0.52	0.89 ± 0.51	0.37 ± 0.38
NEVIS	**Winter**	**-1.04 ± 0.19**	**-0.77 ± 0.38**	**1.35 ± 0.17**	0.25 ± 0.28	-0.42 ± 0.31	-0.51 ± 0.30	**1.05 ± 0.31**	0.04 ± 0.24	0.18 ± 0.36	-0.13 ± 0.29
	L. Winter	**-1.01 ± 0.13**	-0.04 ± 0.18	**0.51 ± 0.13**	-0.43 ± 0.24	**-0.47 ± 0.23**	-0.09 ± 0.17	0.27 ± 0.20	0.24 ± 0.17	**1.11 ± 0.18**	-0.08 ± 0.22
	Denning	-0.25 ± 0.15	-0.53 ± 0.39	**1.17 ± 0.15**	**0.64 ± 0.21**	-0.18 ± 0.31	-0.05 ± 0.19	-0.55 ± 0.31	0.08 ± 0.39	0.40 ± 0.56	**-0.74 ± 0.37**
	L. Summer	-0.22 ± 0.22	-0.61 ± 0.50	**1.12 ± 0.22**	**1.10 ± 0.25**	**-1.96 ± 0.68**	0.02 ± 0.27	**0.70 ± 0.26**	-0.76 ± 0.67	-0.13 ± 0.93	**0.74 ± 0.32**
	Fall	**-1.07 ± 0.17**	-0.24 ± 0.29	**1.07 ± 0.15**	-0.12 ± 0.18	-0.62 ± 0.32	0.10 ± 0.19	-0.06 ± 0.20	**0.57 ± 0.21**	0.23 ± 0.36	0.16 ± 0.22

[a] Winter = 1 January - 28 February, Late Winter = 1 March - 31 April, Denning = 1 May - 31 July, Late Summer = 1 August - 30 September, Fall = 1 October - 31 December.

[b] There are no selection coefficients for habitat classes because models based on NDVI (Habitat Biomass) were ranked highest as the likely best models describing resource selection by the Pocketknife and Lower Besa packs during denning.

[c] There are no selection coefficients for habitat classes because habitat models based on relative prey quality were ranked highest as the likely best models describing resource selection by the Richards pack during fall 2002.

Table 3.5. Resource selection coefficients (± SE) representing seasonal selection patterns across wolves (global) and by wolf pack for landscape features in the Besa-Prophet study area of northern British Columbia. Coefficients are based on pooled data between 2001 and 2004 (unless otherwise indicated). Values in bold indicate significant selection (positive values) or avoidance (negative values) as determined by 95 % confidence intervals. NAS = No Aspect (<1° slope). Blanks indicate those variables/parameters that were not included in final model rankings or could not be tested because of zero use.

		FRAGMENTATION [b]			ASPECT				
PACK	Season [a]	Low	Medium	High	N	E	S	W	NAS
GLOBAL	**Winter**	**-0.20 ± 0.07**	-0.03 ± 0.05	**0.23 ± 0.05**	0.10 ± 0.07	-0.11 ± 0.07	-0.02 ± 0.07	**-0.31 ± 0.09**	**0.33 ± 0.12**
	Late Winter	**-0.15 ± 0.05**	0.01 ± 0.04	**0.14 ± 0.04**	**-0.40 ± 0.06**	**-0.20 ± 0.05**	**0.34 ± 0.05**	-0.01 ± 0.06	**0.27 ± 0.08**
	Denning	-0.08 ± 0.04	-0.05 ± 0.04	**0.13 ± 0.04**	**0.17 ± 0.05**	**-0.20 ± 0.05**	**0.27 ± 0.05**	**-0.39 ± 0.06**	0.15 ± 0.08
	Late Summer	-0.09 ± 0.06	-0.02 ± 0.04	**0.10 ± 0.05**	**0.34 ± 0.07**	0.05 ± 0.07	-0.06 ± 0.07	-0.03 ± 0.09	**-0.30 ± 0.11**
	Fall	**-0.11 ± 0.05**	0.04 ± 0.04	**0.08 ± 0.04**	**0.19 ± 0.06**	-0.11 ± 0.06	**-0.15 ± 0.06**	**-0.16 ± 0.08**	**0.22 ± 0.12**
LOWER-BESA	**Winter**	-0.009 ± 0.04	-0.02 ± 0.04	0.03 ± 0.04	0.009 ± 0.02	0.002 ± 0.01	-0.03 ± 0.03	-0.0006 ± 0.02	0.02 ± 0.02
	Late Winter	0.03 ± 0.12	**-0.30 ± 0.11**	**0.28 ± 0.10**	**-0.47 ± 0.16**	-0.24 ± 0.13	**0.96 ± 0.14**	-0.13 ± 0.17	-0.12 ± 0.21
	Denning	**-0.43 ± 0.18**	-0.16 ± 0.13	**0.59 ± 0.11**	**-0.51 ± 0.15**	0.10 ± 0.13	**0.57 ± 0.15**	0.25 ± 0.15	**-0.41 ± 0.19**
	Late Summer	-0.22 ± 0.20	-0.06 ± 0.15	**0.28 ± 0.15**	-0.02 ± 0.12	-0.03 ± 0.12	-0.12 ± 0.17	-0.19 ± 0.19	0.36 ± 0.26
	Fall	0.01 ± 0.01	-0.01 ± 0.01	-0.001 ± 0.01	0.06 ± 0.06	0.01 ± 0.05	0.001 ± 0.05	-0.11 ± 0.09	0.04 ± 0.08
POCKET-KNIFE	**Winter**	-0.19 ± 0.13	-0.14 ± 0.11	**0.32 ± 0.10**	0.15 ± 0.15	0.24 ± 0.13	-0.09 ± 0.15	**-0.83 ± 0.22**	**0.52 ± 0.18**
	Late Winter	-0.08 ± 0.08	-0.009 ± 0.05	0.09 ± 0.06	-0.16 ± 0.14	-0.21 ± 0.14	-0.08 ± 0.15	-0.17 ± 0.17	**0.63 ± 0.16**
	Denning	-0.02 ± 0.04	-0.01 ± 0.03	0.03 ± 0.03	-0.04 ± 0.13	**0.39 ± 0.12**	-0.06 ± 0.17	**-0.53 ± 0.18**	0.23 ± 0.17
	Late Summer	-0.29 ± 0.20	-0.16 ± 0.15	**0.45 ± 0.15**					
	Fall	**-0.40 ± 0.19**	0.08 ± 0.13	**0.32 ± 0.13**	0.16 ± 0.10	-0.02 ± 0.07	-0.04 ± 0.09	-0.07 ± 0.10	-0.02 ± 0.11
DOPP	**Late Winter**	**-0.47 ± 0.17**	**0.36 ± 0.12**	0.11 ± 0.12	-0.33 ± 0.20	-0.28 ± 0.18	0.15 ± 0.16	**0.57 ± 0.19**	-0.11 ± 0.32
	Denning	-0.007 ± 0.03	-0.01 ± 0.02	0.02 ± 0.02	-0.10 ± 0.17	-0.23 ± 0.17	**0.48 ± 0.15**	**-0.93 ± 0.30**	**0.78 ± 0.24**
	Late Summer	-0.01 ± 0.02	-0.001 ± 0.03	0.01 ± 0.02	0.13 ± 0.10	0.03 ± 0.07	-0.003 ± 0.07	-0.14 ± 0.13	-0.01 ± 0.13
	Fall	-0.06 ± 0.07	-0.008 ± 0.05	0.06 ± 0.06					
KEILY	**Winter**	-0.06 ± 0.07	0.008 ± 0.05	0.05 ± 0.06	0.09 ± 0.17	-0.10 ± 0.17	0.04 ± 0.16	-0.43 ± 0.28	0.41 ± 0.48
	Late Winter	**-0.28 ± 0.10**	0.15 ± 0.08	0.13 ± 0.08	**-0.55 ± 0.14**	-0.15 ± 0.13	**0.27 ± 0.11**	0.26 ± 0.14	0.17 ± 0.22
	Denning	-0.04 ± 0.10	**0.22 ± 0.10**	-0.19 ± 0.10	**-0.36 ± 0.18**	**-0.41 ± 0.17**	**0.30 ± 0.15**	**-0.44 ± 0.23**	**0.91 ± 0.36**
RICHARDS	**Late Winter**	-0.07 ± 0.07	0.06 ± 0.06	0.01 ± 0.05	**-0.55 ± 0.26**	-0.27 ± 0.27	0.29 ± 0.23	**0.99 ± 0.33**	-0.45 ± 0.45
	Denning	0.01 ± 0.03	-0.02 ± 0.02	0.01 ± 0.02	0.18 ± 0.13	-0.01 ± 0.11	0.20 ± 0.12	**-0.43 ± 0.20**	0.06 ± 0.22
	Late Summer	0.001 ± 0.03	-0.004 ± 0.02	0.003 ± 0.02	-0.001 ± 0.009	-0.005 ± 0.009	-0.001 ± 0.008	0.007 ± 0.01	0.001 ± 0.02
	Fall [c]								
PROPHET	**Winter**	**-0.42 ± 0.19**	-0.05 ± 0.14	**0.47 ± 0.13**	0.06 ± 0.08	-0.12 ± 0.11	0.01 ± 0.08	-0.14 ± 0.12	0.19 ± 0.19
	Late Winter	-0.02 ± 0.03	0.001 ± 0.02	0.02 ± 0.03	**-0.52 ± 0.17**	0.15 ± 0.16	**0.45 ± 0.15**	-0.27 ± 0.20	0.19 ± 0.30
	Denning	-0.08 ± 0.09	-0.09 ± 0.08	0.16 ± 0.09	-0.01 ± 0.02	0.0001 ± 0.02	0.02 ± 0.02	-0.03 ± 0.03	0.01 ± 0.04
	Fall	**-0.49 ± 0.18**	0.06 ± 0.14	**0.43 ± 0.15**	-0.01 ± 0.02	0.02 ± 0.02	-0.01 ± 0.02	-0.02 ± 0.03	0.02 ± 0.04
NEVIS	**Winter**	-0.04 ± 0.04	0.01 ± 0.03	0.02 ± 0.03	0.01 ± 0.03	-0.04 ± 0.03	0.01 ± 0.02	0.03 ± 0.03	-0.01 ± 0.05
	Late Winter	-0.03 ± 0.03	0.02 ± 0.02	0.008 ± 0.02	-0.16 ± 0.09	-0.03 ± 0.07	0.10 ± 0.07	0.02 ± 0.08	0.08 ± 0.13
	Denning	0.02 ± 0.04	0.02 ± 0.03	-0.04 ± 0.03	**0.92 ± 0.11**	**-0.40 ± 0.13**	0.18 ± 0.12	-0.25 ± 0.16	**-0.45 ± 0.20**
	Late Summer	-0.02 ± 0.09	0.14 ± 0.08	-0.12 ± 0.08	**0.82 ± 0.13**	-0.14 ± 0.14	**-0.30 ± 0.15**	0.19 ± 0.15	**-0.57 ± 0.23**
	Fall	-0.05 ± 0.09	**0.21 ± 0.08**	**-0.16 ± 0.08**	**0.26 ± 0.12**	**-0.24 ± 0.12**	**-0.23 ± 0.11**	-0.24 ± 0.15	**0.45 ± 0.22**

[a] Winter = 1 January - 28 February, Late Winter = 1 March - 31 April, Denning = 1 May - 31 July, Late Summer = 1 August - 30 September, Fall = 1 October - 31 December.

[b] Fragmentation is an index of vegetative diversity (see text).

[c] There are no selection coefficients for landscape features because models based on relative prey quality were ranked highest as the likely best models describing resource selection by the Richards pack during fall 2002.

Table 4.4. Habitat classes and their selection coefficients ($\beta_i \pm$ SE) from the best resource selection models by season for individual female grizzly bears in the Besa-Prophet study area of northern British Columbia. Coefficients are based on pooled data between 2001 and 2004. Values in bold indicate significant selection (positive values) or avoidance (negative values) as determined by 95 % confidence intervals.

Bear	Season[a]	Conifer	Stunted Spruce	Shrub	Alpine Shrub	Non-Vegetated	Riparian Spruce	Open Alpine	Deciduous Burns	*Elymus* Burns	Sub-Alpine Spruce	Biomass[b]	Quality[c]	B x Q[d]
G01A	Spring	**-0.45 ± 0.19**	0.27 ± 0.24	**-1.18 ± 0.52**	**0.73 ± 0.17**	0.22 ± 0.17		0.06 ± 0.17	-0.14 ± 0.20	0.26 ± 0.21	0.24 ± 0.22	**-0.15 ± 0.07**		
	Summer	**-0.63 ± 0.23**	-0.36 ± 0.27	0.15 ± 0.30	**0.45 ± 0.22**	0.02 ± 0.28	0.23 ± 0.31	**-0.47 ± 0.24**	0.13 ± 0.26	**0.55 ± 0.28**	-0.08 ± 0.27			
	Fall	**-0.85 ± 0.34**	0.09 ± 0.37	-0.24 ± 0.40	0.19 ± 0.40	0.09 ± 0.44	-0.42 ± 0.44	-0.33 ± 0.50	0.40 ± 0.36	**1.17 ± 0.37**	-0.11 ± 0.39			
G05A	Spring	-0.36 ± 0.39	-0.15 ± 0.50	-0.16 ± 0.59	0.42 ± 0.45	-0.60 ± 0.47	**-1.73 ± 0.80**	**0.86 ± 0.41**	0.61 ± 0.39	**0.81 ± 0.42**	0.29 ± 0.49			
	Summer	**-0.92 ± 0.23**	**-1.10 ± 0.38**	**0.99 ± 0.22**	**0.85 ± 0.22**	**-1.94 ± 0.51**	0.11 ± 0.23	**-0.61 ± 0.29**	**0.90 ± 0.19**	**0.44 ± 0.22**	**1.39 ± 0.25**			
	Fall	**-0.94 ± 0.41**	-0.47 ± 0.46	0.29 ± 0.40	-0.13 ± 0.67	-0.14 ± 0.52	0.06 ± 0.42	0.27 ± 0.65	0.30 ± 0.42	0.47 ± 0.47	0.28 ± 0.52			
G08A	Spring	**-0.51 ± 0.14**	-0.30 ± 0.27	-0.07 ± 0.20	**0.44 ± 0.18**	-0.14 ± 0.15	0.003 ± 0.20	0.23 ± 0.25	-0.02 ± 0.22	**0.81 ± 0.30**	**-0.45 ± 0.19**	**-0.25 ± 0.12**		
	Summer	-0.25 ± 0.39	-1.39 ± 0.76	**0.89 ± 0.44**	0.80 ± 0.43	**-0.92 ± 0.46**	0.60 ± 0.49	**-1.22 ± 0.61**	**1.14 ± 0.44**	-0.10 ± 0.62	0.45 ± 0.42			
	Fall	-0.58 ± 0.36	-0.46 ± 0.57	0.74 ± 0.40	**1.04 ± 0.41**	**-1.39 ± 0.50**	0.44 ± 0.44	-0.50 ± 0.56	-0.22 ± 0.49	0.68 ± 0.48	0.24 ± 0.40			
G15B	Spring	-0.22 ± 0.15	0.23 ± 0.16	-0.46 ± 0.37	-0.55 ± 0.35	0.06 ± 0.16	**0.60 ± 0.31**	0.07 ± 0.17	0.01 ± 0.16	**0.44 ± 0.22**	-0.19 ± 0.23	**-0.72 ± 0.34**		
	Summer	**-0.80 ± 0.19**	**-0.70 ± 0.23**	0.45 ± 0.38	-0.27 ± 0.44	**-0.74 ± 0.30**	-0.03 ± 0.26	-0.21 ± 0.33	**0.79 ± 0.22**	0.41 ± 0.26	**1.10 ± 0.25**			
	Fall	-0.57 ± 0.46	0.12 ± 0.49	0.87 ± 0.52	-0.51 ± 0.74	-0.52 ± 0.65	0.28 ± 0.52	**-2.01 ± 0.86**	0.23 ± 0.60	0.89 ± 0.57	**1.21 ± 0.50**			
G18B	Spring	-0.28 ± 0.32	0.12 ± 0.38	-0.22 ± 0.40	-0.06 ± 0.33	0.25 ± 0.38	0.16 ± 0.50	-0.06 ± 0.35	-0.26 ± 0.37	0.69 ± 0.38	-0.33 ± 0.37	**-0.55 ± 0.27**		
	Summer	**-0.64 ± 0.12**	**-0.73 ± 0.20**	-0.11 ± 0.22	**0.83 ± 0.11**	**-1.13 ± 0.27**	-0.03 ± 0.25	**-0.33 ± 0.14**	**0.64 ± 0.16**	**0.91 ± 0.22**	**0.58 ± 0.14**			
	Fall	**-0.51 ± 0.13**	-0.12 ± 0.19	**0.39 ± 0.16**	**0.51 ± 0.22**	-0.38 ± 0.27	0.36 ± 0.21	**-0.78 ± 0.39**	0.27 ± 0.16	0.04 ± 0.28	0.21 ± 0.18			
G20A	Spring	0.11 ± 0.15	0.31 ± 0.23	-0.11 ± 0.39	-0.23 ± 0.23	**-0.68 ± 0.36**	0.60 ± 0.35	**-0.65 ± 0.33**	0.35 ± 0.25	0.21 ± 0.34	0.11 ± 0.29	0.40 ± 0.27		
	Summer	-0.17 ± 0.15	0.15 ± 0.22	-0.08 ± 0.24	0.17 ± 0.23	**-1.08 ± 0.39**	**0.55 ± 0.25**	**-0.97 ± 0.30**	0.04 ± 0.26	**0.75 ± 0.29**	**0.64 ± 0.21**			
	Fall	**-0.49 ± 0.16**	-0.36 ± 0.22	0.07 ± 0.20	**0.66 ± 0.28**	-0.06 ± 0.28	0.03 ± 0.25	-0.43 ± 0.48	0.04 ± 0.21	0.02 ± 0.29	**0.52 ± 0.23**			
G21A	Spring											**-9.72 ± 1.84**		
	Summer	**-0.79 ± 0.30**	0.45 ± 0.94	-0.22 ± 0.30	**0.51 ± 0.21**	**-1.05 ± 0.27**	-0.47 ± 0.46	**-0.83 ± 0.30**	**1.18 ± 0.22**	**1.23 ± 0.30**	-0.02 ± 0.24			
	Fall	**-0.81 ± 0.30**	-0.55 ± 1.04	0.05 ± 0.33	**0.60 ± 0.25**	0.26 ± 0.23	0.16 ± 0.40	-0.62 ± 0.38	-0.25 ± 0.27	**1.15 ± 0.36**	0.01 ± 0.25			
G22A	Spring	-0.09 ± 0.32	-0.67 ± 0.66		-0.21 ± 0.35	**0.91 ± 0.28**		**1.72 ± 0.24**	-0.87 ± 0.69	0.14 ± 0.47	-0.92 ± 0.67			
	Summer	-0.27 ± 0.14	**-0.75 ± 0.30**	0.36 ± 0.30	**0.32 ± 0.15**	**-1.31 ± 0.26**	-0.40 ± 0.26	**-1.28 ± 0.28**	**0.82 ± 0.28**	**1.59 ± 0.26**	**0.91 ± 0.16**			
	Fall	-0.24 ± 0.16	-0.38 ± 0.27	0.39 ± 0.27	0.13 ± 0.23	**-1.05 ± 0.36**	**-0.75 ± 0.33**	0.26 ± 0.30	0.08 ± 0.28	**1.38 ± 0.26**	0.18 ± 0.23			
G23A	Spring	0.12 ± 0.19	0.28 ± 0.38	0.01 ± 0.19	-0.21 ± 0.22	-0.01 ± 0.14	-0.23 ± 0.47	0.23 ± 0.23	-0.01 ± 0.16	-0.21 ± 0.32	0.03 ± 0.22	0.52 ± 0.96		
	Summer	**-0.82 ± 0.29**	0.91 ± 0.67	0.38 ± 0.32	0.27 ± 0.25	**-1.42 ± 0.35**	0.64 ± 0.52	**-0.77 ± 0.35**	0.28 ± 0.25	0.75 ± 0.41	-0.21 ± 0.32			**0.21 ± 0.10**
	Fall	**-1.44 ± 0.42**		-0.25 ± 0.49	1.09 ± 0.62	-0.02 ± 0.68	-1.14 ± 0.76	**2.32 ± 0.61**	-1.70 ± 1.02	0.40 ± 0.61	0.74 ± 0.56			
G24A	Spring	**-1.18 ± 0.42**	0.06 ± 0.64		**0.89 ± 0.39**	-0.83 ± 0.55	-0.35 ± 1.04	0.33 ± 0.43	0.67 ± 0.47	0.95 ± 0.59	-0.55 ± 0.49			
	Summer	**-1.54 ± 0.32**	**-1.07 ± 0.43**	0.68 ± 0.57	**2.02 ± 0.21**	**-2.19 ± 0.45**	0.33 ± 0.49	0.19 ± 0.25	**1.49 ± 0.35**	-0.32 ± 1.03	0.42 ± 0.31			
	Fall	0.09 ± 0.13	**0.59 ± 0.21**	-0.36 ± 0.41	**-0.64 ± 0.23**	-0.12 ± 0.22	-0.31 ± 0.29	-0.13 ± 0.25	-0.06 ± 0.27	**1.33 ± 0.24**	-0.39 ± 0.28			

Table 4.4 Continued

Bear	Season[a]	Conifer	Stunted Spruce	Shrub	Alpine Shrub	Non-Vegetated	Riparian Spruce	Open Alpine	Deciduous Burns	*Elymus* Burns	Sub-Alpine Spruce	Biomass[b]	Quality[c]	B x Q[d]
G25A	Spring	**-1.44 ± 0.56**	-0.33 ± 0.99	0.40 ± 0.45	0.05 ± 0.23	**-0.76 ± 0.27**	0.70 ± 0.52	-0.23 ± 0.29	**1.38 ± 0.29**	**1.10 ± 0.32**	-0.86 ± 0.50			
	Summer	**-1.45 ± 0.28**	0.04 ± 0.48	**0.45 ± 0.21**	**0.94 ± 0.14**	**-1.23 ± 0.24**	-0.44 ± 0.39	**-0.55 ± 0.19**	**1.43 ± 0.19**	**1.38 ± 0.24**	-0.30 ± 0.30			
	Fall	**-0.52 ± 0.16**	**0.80 ± 0.32**	**0.41 ± 0.16**	-0.05 ± 0.16	**-0.86 ± 0.25**	-0.03 ± 0.23	**-0.61 ± 0.26**	**0.90 ± 0.18**	0.18 ± 0.23	-0.23 ± 0.24			
G26A	Spring	-0.24 ± 0.33	-0.26 ± 0.67	-0.45 ± 0.72	**-0.74 ± 0.29**	-0.16 ± 0.24	**2.24 ± 0.60**	-0.21 ± 0.28	-0.54 ± 0.43	0.49 ± 0.35	-0.15 ± 0.43			
	Summer	**-0.82 ± 0.24**	0.44 ± 0.28	-0.51 ± 0.28	**1.02 ± 0.15**	**-1.13 ± 0.23**	-0.11 ± 0.34	-0.01 ± 0.20	**1.14 ± 0.22**	**0.53 ± 0.26**	-0.56 ± 0.31			
	Fall	0.23 ± 0.19	-0.17 ± 0.46	**0.83 ± 0.26**	**-0.43 ± 0.19**	**-1.35 ± 0.29**	0.10 ± 0.33	**-0.93 ± 0.29**	0.58 ± 0.35	**1.66 ± 0.23**	-0.50 ± 0.34			
G27A[e]	Spring	-0.87 ± 0.55	**1.014 ± 0.38**	-0.39 ± 1.34	0.6 ± 1.07	0.11 ± 0.46	-0.11 ± 0.55	-1.30 ± 1.12	**1.01 ± 0.39**	**1.07 ± 0.41**	-1.13 ± 0.97			
	Summer												**0.96 ± 0.47**	
	Fall	**0.47 ± 0.21**	-0.50 ± 0.38	**0.99 ± 0.26**		**-2.24 ± 0.90**	0.09 ± 0.30	**-1.53 ± 0.66**	**1.19 ± 0.25**	**1.54 ± 0.32**				
2001	Spring	**-0.50 ± 0.17**	0.04 ± 0.28	0.16 ± 0.25	-0.23 ± 0.22	-0.03 ± 0.19	0.39 ± 0.35	**0.69 ± 0.23**	-0.17 ± 0.20	**0.36 ± 0.21**	**-0.71 ± 0.27**	**-0.47 ± 0.22**		
	Summer	-0.49 ± 0.34	-0.66 ± 0.46	0.43 ± 0.39	0.46 ± 0.36	**-1.42 ± 0.49**	-0.09 ± 0.46	-0.83 ± 0.44	**1.02 ± 0.35**	0.72 ± 0.41	**0.85 ± 0.36**			
	Fall	**-0.85 ±0.11**	-0.12 ± 0.14	**0.46 ± 0.12**	**0.63 ± 0.16**	**-0.43 ± 0.19**	0.01 ± 0.14	-0.46 ± 0.25	0.12 ± 0.13	**0.32 ± 0.16**	**0.32 ± 0.14**			
2002	Spring	-0.24 ± 0.13	-0.32 ± 0.24	-0.13 ± 0.31	0.21 ± 0.16	**-0.88 ± 0.17**	0.23 ± 0.30	**-0.36 ± 0.18**	**0.48 ± 0.15**	**0.87 ± 0.19**	0.13 ± 0.21			
	Summer	**-0.78 ± 0.09**	-0.23 ± 0.15	**0.32 ± 0.10**	**0.88 ± 0.08**	**-1.40 ± 0.16**	-0.01 ± 0.14	**-0.52 ± 0.12**	**0.71 ± 0.10**	**0.65 ± 0.13**	**0.38 ± 0.10**			
	Fall	**-0.57 ± 0.07**	-0.11 ± 0.11	0.03 ± 0.09	**0.28 ± 0.09**	-0.18 ± 0.11	**-0.23 ± 0.11**	-0.11 ± 0.13	0.08 ± 0.09	**0.84 ± 0.10**	-0.04 ± 0.11			
2003	Spring	**-0.50 ± 0.09**	0.20 ± 0.15	**-0.68 ± 0.16**	-0.09 ± 0.09	**0.32 ± 0.09**	-0.06 ± 0.18	**0.48 ± 0.10**	**0.24 ± 0.11**	**0.67 ± 0.12**	**-0.57 ± 0.13**			
	Summer	**-0.58 ± 0.07**	**-0.57 ± 0.12**	-0.17 ± 0.10	**0.95 ± 0.08**	**-0.97 ± 0.13**	-0.11 ± 0.12	**-0.46 ± 0.11**	**0.76 ± 0.09**	**0.66 ± 0.11**	**0.48 ± 0.09**			
	Fall	**-0.31 ± 0.06**	**-0.26 ± 0.10**	**0.59 ± 0.08**	0.05 ± 0.09	**-0.66 ± 0.11**	0.18 ± 0.11	**-0.91 ± 0.14**	**0.35 ± 0.09**	**0.69 ± 0.10**	**0.27 ± 0.09**			
2004	Spring	**-0.48 ± 0.11**	**0.68 ± 0.13**	**-0.98 ± 0.24**	-0.11 ± 0.12	0.18 ± 0.12	**0.45 ± 0.20**	**-0.32 ± 0.12**	0.13 ± 0.13	**0.84 ± 0.13**	**-0.39 ± 0.15**			
	Summer	-0.50 ± 0.29	-0.33 ± 0.32	0.27 ± 0.33	**0.67 ± 0.28**	**-0.90 ± 0.35**	0.37 ± 0.33	-0.13 ± 0.25	0.31 ± 0.30	0.24 ± 0.32	-0.003 ± 0.29		**0.89 ± 0.34**	
	Fall	**-1.07 ± 0.19**	**-0.97 ± 0.25**	**0.75 ± 0.20**	**0.54 ± 0.24**	-0.32 ± 0.25	**0.63 ± 0.25**	-0.30 ± 0.31	0.30 ± 0.22	**1.10 ± 0.20**	**-0.65 ± 0.32**			

[a] Spring = den emergence - 15 June; Summer = 16 June - 15 August; Fall = 16 August - denning.
[b] As measured by absolute NDVI. Peak June values were used for spring models, peak July values were used for summer models, and peak September values were used for fall models.
[c] As measured by the change in NDVI. Due to inconsistent satellite data, habitat quality was only used in summer models and defined as the change from peak June values to peak July values.
[d] A measure of the interaction of available biomass (indexed by absolute NDVI) and habitat quality (indexed by the change from peak June NDVI to peak July NDVI values). Only used in summer models.
[e] *Based on 1 year of data.*

Table 4.5. Resource selection coefficients ($\beta_i \pm$ SE) for topographical features and vegetative diversity (fragmentation) from the best resource selection models by season for individual female grizzly bears in the Besa-Prophet study area of northern British Columbia. Coefficients are based on pooled data between 2001 and 2004 (unless otherwise indicated). Values in bold indicate significant selection (positive values) or avoidance (negative values) as determined by 95 % confidence intervals. NAS = No Aspect (< 1° slope).

		Elevation[b]		Fragmentation			Aspect				
Bear	**Season[a]**	**km**	**km²**	**Low**	**Medium**	**High**	**N**	**E**	**S**	**W**	**No Aspect**
G01A	**Spring**	**8.50 ± 3.82**	**-2.35 ± 1.08**	-0.08 ± 0.09	-0.04 ± 0.06	0.13 ± 0.07	**-0.77 ± 0.18**	0.14 ± 0.12	**0.33 ± 0.11**	**0.30 ± 0.11**	
	Summer			0.02 ± 0.19	-0.09 ± 0.18	0.08 ± 0.17	**0.43 ± 0.22**	-0.35 ± 0.22	**-0.44 ± 0.22**	-0.35 ± 0.24	**0.72 ± 0.36**
	Fall	**21.60 ± 2.02**	**-8.20 ± 1.19**	-0.22 ± 0.28	0.03 ± 0.25	0.19 ± 0.25	-0.20 ± 0.32	-0.03 ± 0.29	0.19 ± 0.29	0.16 ± 0.31	-0.11 ± 0.46
G05A	**Spring**			0.05 ± 0.21	-0.13 ± 0.21	0.07 ± 0.19	-0.21 ± 0.38	-0.01 ± 0.32	0.45 ± 0.31	-0.22 ± 0.36	
	Summer	-1.57 ± 0.91	0.60 ± 0.34	**0.25 ± 0.08**	-0.08 ± 0.08	**-0.18 ± 0.08**	**0.43 ± 0.15**	-0.19 ± 0.12	-0.23 ± 0.13	**0.33 ± 0.14**	-0.30 ± 0.28
	Fall	**20.46 ± 2.32**	**-8.41 ± 1.43**	-0.17 ± 0.29	0.005 ± 0.26	0.17 ± 0.25	0.05 ± 0.34	-0.33 ± 0.35	-0.18 ± 0.33	**0.83 ± 0.33**	-0.37 ± 0.47
G08A	**Spring**	**32.76 ± 6.84**	**-11.61 ± 2.27**	**-0.24 ± 0.11**	-0.05 ± 0.09	**0.29 ± 0.08**	-0.13 ± 0.11	0.18 ± 0.12	**0.32 ± 0.12**	-0.02 ± 0.12	-0.35 ± 0.26
	Summer	**46.78 ± 3.00**	**-15.40 ± 1.72**	-0.05 ± 0.12	0.008 ± 0.10	0.04 ± 0.10	-0.26 ± 0.35	0.002 ± 0.34	0.17 ± 0.33	-0.35 ± 0.37	0.44 ± 0.50
	Fall	**42.23 ± 2.39**	**-15.17 ± 1.37**	0.32 ± 0.30	-0.26 ± 0.28	-0.06 ± 0.27	-0.01 ± 0.27	0.17 ± 0.29	0.26 ± 0.28	-0.08 ± 0.31	-0.34 ± 0.40
G15B	**Spring**	**21.25 ± 6.00**	**-6.82 ± 1.99**	-0.01 ± 0.02	-0.003 ± 0.02	0.01 ± 0.02	0.02 ± 0.05	0.07 ± 0.06	-0.06 ± 0.06	0.05 ± 0.05	-0.09 ± 0.15
	Summer	0.40 ± 3.80	-0.56 ± 1.38	0.04 ± 0.04	-0.04 ± 0.04	0.002 ± 0.03	**0.30 ± 0.16**	0.08 ± 0.15	**-1.01 ± 0.22**	-0.07 ± 0.20	0.69 ± 0.38
	Fall			-0.18 ± 0.45	-0.21 ± 0.40	0.39 ± 0.37	0.14 ± 0.25	-0.13 ± 0.26	0.07 ± 0.25	-0.25 ± 0.31	0.18 ± 0.37
G18B	**Spring**	**32.46 ± 2.51**	**-10.19 ± 1.36**	**-0.74 ± 0.38**	0.15 ± 0.31	**0.60 ± 0.30**	-0.50 ± 0.45	-0.25 ± 0.43	0.61 ± 0.42	0.29 ± 0.43	-0.16 ± 0.78
	Summer			-0.06 ± 0.06	-0.05 ± 0.05	0.11 ± 0.06	**0.67 ± 0.11**	**-0.33 ± 0.12**	**-0.60 ± 0.13**	**-0.42 ± 0.14**	**0.68 ±0.33**
	Fall	**31.43 ± 5.59**	**-11.77 ± 1.95**	**-0.21 ± 0.09**	0.04 ± 0.07	**0.18 ± 0.07**	0.12 ± 0.12	**-0.23 ± 0.12**	**0.23 ± 0.11**	**0.34 ± 0.13**	-0.46 ± 0.27
G20A	**Spring**			-0.03 ± 0.04	0.01 ± 0.03	0.02 ± 0.03	0.04 ± 0.15	0.01 ± 0.15	**-0.46 ± 0.22**	0.03 ± 0.16	0.38 ± 0.41
	Summer	-0.86 ± 1.04	0.31 ± 0.36	-0.03 ± 0.03	0.004 ± 0.02	0.02 ± 0.03	0.24 ± 0.14	-0.26 ± 0.14	-0.26 ± 0.15	-0.32 ± 0.17	**0.60 ± 0.29**
	Fall	**18.20 ± 6.13**	**-7.28 ± 2.15**	0.01 ± 0.03	-0.02 ± 0.02	0.005 ± 0.02	-0.0002 ± 0.01	-0.01 ± 0.02	0.009 ± 0.01	-0.009 ± 0.02	0.01 ± 0.03
G21A	**Spring**	14.05 ± 11.44	-5.90 ± 3.30	0.006 ± 0.03	-0.03 ± 0.04	0.02 ± 0.04	**-0.76 ± 0.26**	**0.35 ± 0.18**	**0.71 ± 0.22**	-0.30 ± 0.22	
	Summer	**38.56 ± 9.14**	**-11.61 ± 2.78**	**-0.39 ± 0.12**	-0.06 ± 0.10	**0.44 ± 0.10**					
	Fall	**49.84 ± 8.95**	**-16.22 ± 2.63**	-0.09 ± 0.12	**-0.33 ± 0.12**	**0.42 ± 0.11**	-0.006 ± 0.15	**0.31 ± 0.16**	0.19 ± 0.15	-0.21 ± 0.17	-0.29 ± 0.45
G22A	**Spring**			**-0.85 ± 0.19**	**0.34 ± 0.15**	**0.51 ± 0.15**	-0.25 ± 0.22	**0.41 ± 0.16**	**0.44 ± 0.18**	**-0.61 ± 0.25**	
	Summer	0.86 ± 0.65	-0.28 ± 0.22	-0.12 ± 0.08	0.12 ± 0.07	-0.004 ± 0.06	0.23 ± 0.13	-0.12 ± 0.14	**-0.69 ± 0.15**	**0.36 ± 0.17**	0.23 ± 0.36
	Fall	**10.07 ± 5.25**	**-4.20 ± 1.74**	-0.02 ± 0.03	0.03 ± 0.03	-0.02 ± 0.03	-0.07 ± 0.14	0.16 ± 0.14	**-0.35 ± 0.16**	-0.06 ± 0.17	0.32 ± 0.39
G23A	**Spring**	10.93 ± 8.46	-4.17 ± 2.62	-0.45 ± 0.26	**0.53 ± 0.21**	-0.07 ± 0.21	-0.12 ± 0.14	0.004 ± 0.10	0.30 ± 0.19	-0.19 ± 0.17	
	Summer	**31.49 ± 6.58**	**-9.25 ± 1.86**	-0.002 ± 0.02	0.003 ± 0.01	-0.001 ± 0.02	**0.72 ± 0.24**	**-0.10 ± 0.25**	0.10 ± 0.25	0.26 ± 0.25	-0.97 ± 0.79
	Fall	**-25.44 ± 9.53**	**5.51 ± 2.56**	-0.04 ± 0.06	-0.0005 ± 0.04	0.04 ± 0.05	0.28 ± 0.36	**-1.48 ± 0.40**	**0.79 ± 0.33**	0.23 ± 0.31	0.17 ± 0.72
G24A	**Spring**	**45.45 ± 13.92**	**-13.93 ± 4.20**	**-0.55 ± 0.23**	0.05 ± 0.18	**0.50 ± 0.18**	-0.07 ± 0.08	0.04 ± 0.06	0.05 ± 0.06	-0.02 ± 0.07	
	Summer			-0.08 ± 0.07	0.06 ± 0.06	0.01 ± 0.06	**1.04 ± 0.16**	-0.21 ± 0.14	**-0.78 ± 0.18**	-0.05 ± 0.19	
	Fall	3.91 ± 2.30	**-1.61 ± 0.74**	-0.15 ± 0.0	0.07 ± 0.06	0.08 ± 0.07	**0.72 ± 0.23**	0.26 ± 0.24	**0.45 ± 0.23**	**-0.72 ± 0.31**	-0.71 ± 0.82

Table 4.5 Continued

Bear	Season[a]	Elevation[b]		Fragmentation			Aspect				
		km	km^2	Low	Medium	High	N	E	S	W	NAS
G25A	Spring			**-0.65 ± 0.15**	**0.47 ± 0.13**	0.18 ± 0.14	**-0.56 ± 0.24**	0.18 ± 0.16	**0.78 ± 0.16**	-0.40 ± 0.27	
	Summer	0.37 ± 0.45	0.11 ± 0.13	**-0.46 ± 0.10**	**0.31 ± 0.08**	**0.18 ± 0.09**	**0.48 ± 0.23**	-0.02 ± 0.23	0.21 ± 0.23	**0.74 ± 0.23**	-1.24 ± 0.81
	Fall	**6.98 ± 3.49**	**-2.77 ± 1.07**	-0.02 ± 0.02	0.01 ± 0.02	0.001 ± 0.02	-0.08 ± 0.10	-0.17 ± 0.10	0.11 ± 0.09	-0.06 ± 0.10	0.21 ± 0.19
G26A	Spring			-0.17 ± 0.10	0.001 ± 0.08	0.17 ± 0.10	**-1.16 ± 0.28**	0.33 ± 0.22	0.18 ± 0.22	-0.48 ± 0.28	1.13 ± 0.71
	Summer	**5.46 ± 2.83**	**-1.86 ± 0.83**	**-0.24 ± 0.09**	0.04 ± 0.08	**0.20 ± 0.08**	**-0.56 ± 0.14**	**-0.48 ± 0.13**	-0.09 ± 0.11	-0.12 ± 0.14	**1.25 ± 0.25**
	Fall			**-0.45 ± 0.13**	0.18 ± 0.11	**0.27 ± 0.12**					
G27A	Spring			0.01 ± 0.29	**-0.81 ± 0.24**	**0.80 ± 0.20**	-0.77 ± 0.44	**-0.83 ± 0.33**	**0.63 ± 0.26**	0.01 ± 0.31	0.97 ± 0.78
	Summer	2.70 ± 4.99	-2.23 ± 2.18	-0.13 ± 0.14	-0.05 ± 0.10	0.19 ± 0.12	0.01 ± 0.03	0.02 ± 0.03	0.02 ± 0.04	-0.05 ± 0.05	-0.005 ± 0.05
	Fall	1.50 ± 2.33	-0.46 ± 0.86	0.002 ± 0.03	0.03 ± 0.03	-0.03 ± 0.03	0.14 ± 0.17	0.19 ± 0.16	-0.24 ± 0.18	**-1.08 ± 0.27**	**1.00 ± 0.35**
2001	Spring	**50.1 ± 5.0**	**-16.25 ± 1.68**	**-0.40 ± 0.14**	-0.10 ± 0.11	**0.50 ± 0.10**	-0.26 ± 0.19	-0.002 ± 0.17	**0.33 ± 0.17**	-0.32 ± 0.19	0.26 ± 0.50
	Summer	**11.55 ± 1.56**	**-3.66 ± 0.90**	0.0001 ± 0.04	-0.005 ± 0.04	0.005 ± 0.04	0.34 ± 0.32	-0.16 ± 0.31	-0.18 ± 0.31	-0.14 ± 0.34	0.14 ± 0.49
	Fall	**17.68 ± 2.93**	**-7.062 ± 1.06**	**-0.20 ± 0.08**	-0.02 ± 0.06	**0.21 ± 0.06**	0.11 ± 0.09	**-0.19 ± 0.09**	0.15 ± 0.08	**0.27 ± 0.09**	-0.34 ± 0.18
2002	Spring			-0.004 ± 0.01	-0.004 ± 0.01	0.008 ± 0.01	**-0.48 ± 0.16**	**-0.26 ± 0.13**	-0.03 ± 0.12	-0.02 ± 0.14	**0.78 ± 0.36**
	Summer	**4.83 ± 1.48**	**-1.60 ± 0.46**	**-0.20 ± 0.05**	0.06 ± 0.04	**0.14 ± 0.04**	**0.28 ± 0.07**	-0.12 ± 0.07	**-0.15 ± 0.07**	0.01 ± 0.08	-0.02 ± 0.17
	Fall	**10.99 ± 1.49**	**-4.52 ± 0.50**	-0.006 ± 0.009	0.001 ± 0.007	0.005 ± 0.008	**-0.14 ± 0.06**	-0.08 ± 0.06	**0.12 ± 0.06**	0.05 ± 0.07	0.05 ± 0.13
2003	Spring	**24.85 ± 2.14**	**-7.90 ± 0.66**	**-0.34 ± 0.06**	0.08 ± 0.05	**0.26 ± 0.04**	**-0.24 ± 0.10**	**0.38 ± 0.10**	**0.49 ± 0.09**	-0.01 ± 0.10	**-0.63 ± 0.32**
	Summer	**4.49 ± 1.29**	**-1.75 ± 0.41**	**-0.15 ± 0.05**	0.05 ± 0.04	**0.10 ± 0.04**	**0.25 ± 0.06**	**-0.30 ± 0.06**	**-0.30 ± 0.06**	-0.07 ± 0.07	**0.42 ± 0.13**
	Fall	**17.85 ± 1.73**	**-6.33 ± 0.59**	**-0.12 ± 0.05**	-0.006 ± 0.04	**0.13 ± 0.04**	**0.19 ± 0.06**	-0.08 ± 0.06	0.05 ± 0.06	**-0.17 ± 0.07**	0.007 ± 0.15
2004	Spring	**14.58 ± 1.94**	**-4.26 ± 0.59**	**-0.39 ± 0.08**	-0.06 ± 0.06	**0.44 ± 0.06**	**-0.52 ± 0.12**	-0.11 ± 0.10	**0.29 ± 0.09**	-0.03 ± 0.10	0.38 ± 0.29
	Summer	**-1.76 ± 0.71**	**0.51 ± 0.27**	-0.25 ± 0.27	-0.06 ± 0.24	0.31 ± 0.23	0.17 ± 0.29	-0.27 ± 0.29	-0.29 ± 0.29	-0.30 ± 0.32	0.68 ± 0.46
	Fall	**21.17 ± 4.31**	**-7.97 ± 1.54**	-0.11 ± 0.13	-0.20 ± 0.11	**0.31 ± 0.10**	0.04 ± 0.15	**-0.57 ± 0.15**	**-0.29 ± 0.14**	0.11 ± 0.16	**0.71 ± 0.30**

[a] Spring = den emergence - 15 June; Summer = 16 June - 15 August; Fall = 16 August - denning.
[b] Elevation was entered in competing models as a quadratic function.

Table 5.7. Mean seasonal dietary composition of female (n = 22) and male (n = 12) grizzly bears in the Besa Prophet study area, as determined using mean fractionation values for bears from Hilderbrand et al. (1996). Comparisons are made with average estimates of plant proportions in the diet from Hobson et al. (2000) and an average fractionation value from other studies. x indicates that estimate could not be determined.

		Signature		% Diet Composition												% Plant Estimate	
Bears	Season	δ13C	δ15N	Moose		Elk		Caribou		Sheep		Grazers		Plants		Hobson[1]	Literature[2]
FEMALES				$\bar{X} \pm SD$	range	$\bar{X} \pm SD$	range	$\bar{X} \pm SD$	range	$\bar{X} \pm SD$	range	$\bar{X} \pm SD$	range	$\bar{X} \pm SD$	range		
AB	Spring	-21.95	3.53	6 ± 5	0-22			6 ± 5	0-20			18 ± 5	6-30	70 ± 2	67-74	87	33
	Summer	-22.47	2.45											100		100	x
	Fall	-22.28	4.63	4 ± 4	0-19	30 ± 4	21-41	3 ± 2	0-12	4 ± 4	0-18			59 ± 1	55-62	57	16
AN	Spring	-22.41	2.87											100		100	x
	Summer	-22.65	3.22											100		96	x
	Fall	-22.28	4.41	7 ± 6	0-30	21 ± 5	8-36	4 ± 4	0-19	6 ± 5	0-26			62 ± 2	56-66	63	25
AP	Spring	-22.57	3.32											100		93	x
	Summer	-22.77	3.29											100		94	x
	Fall	-22.37	5.10	4 ± 4	0-18	40 ± 4	31-51	3 ± 2	0-11	4 ± 3	0-17			50 ± 1	46-52	45	15
AR	Spring	-22.51	2.49											100		100	x
	Summer	-22.58	2.83											100		100	x
	Fall	-23.03	4.27	5 ± 4	0-20	22 ± 4	12-34	3 ± 3	0-13	4 ± 4	0-20			66 ± 1	62-69	67	30
AW	Spring	-22.30	3.45	11 ± 7	0-27			7 ± 5	0-20			4 ± 3	0-14	78 ± 2	73-83	90	31
	Summer	-22.59	4.52	10 ± 8	0-42	13 ± 8	0-36	4 ± 3	0-19	9 ± 7	0-32			65 ± 2	58-70	60	18
	Fall	-22.40	5.25	10 ± 8	0-40	32 ± 5	16-47	6 ± 5	0-24	9 ± 7	0-36			44 ± 2	36-48	40	9
BC	Spring	-22.70	2.80											100		100	x
	Summer	-22.84	3.39	5 ± 4	0-20	6 ± 4	0-19	2 ± 2	0-9	4 ± 3	0-15			83 ± 1	80-86	91	44
	Fall	-23.04	4.06	7 ± 6	0-29	14 ± 5	1-29	4 ± 4	0-19	6 ± 5				69 ± 2	63-73	73	33
BN	Spring	-22.45	3.81	5 ± 4	0-18			5 ± 4	0-18			16 ± 5	5-27	73 ± 1	70-76	80	47
	Summer	-22.46	4.36	7 ± 6	0-32	14 ± 7	0-33	2 ± 2	0-12	7 ± 6	0-27			69 ± 2	65-74	65	21
	Fall	-22.75	5.86	6 ± 5	0-24	44 ± 4	33-58	3 ± 3	0-16	5 ± 4	0-23			42 ± 2	37-45	24	4
BS	Spring	-22.07	4.07	6 ± 5	0-22			6 ± 5	0-20			21 ± 5	10-33	67 ± 2	64-71	73	25
	Summer	-22.27	2.97											100		100	x
	Fall	-22.08	4.91	6 ± 5	0-27	32 ± 5	21-47	4 ± 3	0-17	6 ± 5	0-24			52 ± 2	47-56	50	11
BY	Spring	-22.33	2.80											100		100	x
	Summer	-22.33	4.19	7 ± 6	0-30	20 ± 7	0-38	2 ± 2	0-12	7 ± 6	0-31			64 ± 2	60-69	70	25
	Fall	-22.30	4.81	10 ± 8	0-40	23 ± 5	7-38	6 ± 5	0-24	9 ± 7	0-37			53 ± 2	45-57	52	13
C	Spring	-22.84	4.10	7 ± 5	0-23			6 ± 5	0-21			10 ± 5	0-22	77 ± 2	73-81	72	31
	Summer	-23.39	3.72	5 ± 4	0-22	4 ± 4	0-18	3 ± 3	0-14	4 ± 3	0-16			84 ± 2	78-87	82	40
	Fall	-22.61	4.82	9 ± 7	0-37	24 ± 5	8-39	6 ± 5	0-23	9 ± 7	0-36			53 ± 2	46-57	52	22
CG	Spring	-22.29	3.81	12 ± 8	0-34			10 ± 7	0-27			8 ± 5	0-23	71 ± 2	65-75	80	32
	Summer	-22.34	4.22	6 ± 5	0-26	23 ± 6	4-39	2 ± 2	0-9	6 ± 5	0-28			64 ± 2	60-68	69	26
	Fall	-22.58	6.03	3 ± 3	0-16	60 ± 3	52-70	2 ± 2	0-10	3 ± 3	0-15			31 ± 1	28-34	19	1
CZ	Spring	-22.90	1.75											100		100	x
	Summer	-22.87	1.63											100		100	x
	Fall	-22.76	3.79	9 ± 7	0-34	5 ± 4	0-17	6 ± 5	0-24	7 ± 5	0-26			73 ± 2	66-78	80	38

Table 5.7. Continued

		Signature		% Prey Composition												% Plant Estimate	
FEMALES	Season	δ13C	δ15N	Moose mean ± SD	Moose range	Elk mean ± SD	Elk range	Caribou mean ± SD	Caribou range	Sheep mean ± SD	Sheep range	Grazers mean ± SD	Grazers range	Plants mean ± SD	Plants range	Hobson[1]	Literature[2]
L	Spring	-22.95	2.77											100		100	x
	Summer	-23.41	2.05											100		100	x
	Fall	-22.77	4.30	3 ± 3	0-15	26 ± 3	18-35	2 ± 2	0-10	3 ± 3	0-13			66 ± 1	63-68	66	26
M	Spring	-22.88	3.99	6 ± 5	0-20			5 ± 4	0-20			11 ± 5	0-22	78 ± 2	75-81	75	33
	Summer	-22.99	3.92	6 ± 5	0-26	7 ± 5	0-22	3 ± 3	0-15	5 ± 4	0-20			79 ± 2	74-83	77	32
	Fall	-22.69	5.32	6 ± 5	0-25	33 ± 4	22-47	4 ± 3	0-16	5 ± 5	0-22			52 ± 2	47-56	38	11
O	Spring	-22.68	2.82											100		100	x
	Summer	-22.69	2.69											100		100	x
	Fall	-22.41	4.35	4 ± 4	0-18	25 ± 4	16-36	3 ± 2	0-11	4 ± 3	0-17			65 ± 1	61-67	65	24
G01B	Spring	-22.52	3.76	16 ± 9	0-37			10 ± 7	0-28			4 ± 4	0-15	67 ± 3	63-75	81	26
	Summer	-22.71	3.95	9 ± 7	0-37	11 ± 7	0-32	4 ± 3	0-17	8 ± 6	0-29			69 ± 2	63-74	76	31
	Fall	-22.45	4.57	9 ± 7	0-36	20 ± 5	6-35	5 ± 4	0-22	8 ± 6	0-33			58 ± 2	51-62	59	18
G15B	Spring	-21.97	4.55	6 ± 5	0-21			5 ± 4	0-19			32 ± 5	21-43	57 ± 2	54-60	60	10
	Summer	-22.40	4.04	8 ± 7	0-37	15 ± 7	0-34	3 ± 2	0-13	8 ± 6	0-29			67 ± 2	62-72	73	23
	Fall	-22.40	4.85	6 ± 5	0-28	31 ± 5	18-45	4 ± 3	0-17	6 ± 5	0-26			54 ± 2	48-57	51	14
G18B	Spring	-21.93	4.74	15 ± 10	0-42			14 ± 9	0-41			22 ± 6	5-39	49 ± 3	43-55	54	9
	Summer	-22.44	4.01	7 ± 6	0-31	16 ± 7	0-34	2 ± 2	0-11	7 ± 6	0-28			68 ± 2	64-72	74	31
	Fall	-22.51	4.67	6 ± 5	0-23	29 ± 4	18-42	3 ± 3	0-16	5 ± 4	0-21			58 ± 2	53-61	56	17
G26A	Spring	-22.34	4.36	7 ± 6	0-24			7 ± 5	0-25			25 ± 5	12-39	60 ± 2	56-64	65	20
	Summer	-22.51	3.85	7 ± 6	0-33	11 ± 7	0-30	3 ± 3	0-13	7 ± 5	0-26			72 ± 2	67-76	79	35
	Fall	-22.49	4.54	8 ± 6	0-32	21 ± 5	7-36	5 ± 4	0-20	7 ± 6	0-31			59 ± 2	53-63	60	19
G27A	Spring	-22.05	5.03	12 ± 8	0-37			12 ± 8	0-34			24 ± 6	8-40	52 ± 2	47-57	56	7
	Summer	-22.58	4.35	5 ± 4	0-21	28 ± 5	12-42	2 ± 2	0-8	5 ± 5	0-22			61 ± 1	58-64	65	21
	Fall	-22.51	4.44	8 ± 7	0-35	18 ± 5	4-33	5 ± 4	0-22	8 ± 6	0-32			61 ± 2	54-65	62	21
G28A	Spring	-23.09	4.39	18 ± 11	0-47			16 ± 10	0-40			11 ± 6	0-27	55 ± 3	49-62	64	38
	Summer	-23.13	4.51	11 ± 9	0-44	10 ± 7	0-35	6 ± 5	0-23	9 ± 7	0-33			64 ± 3	56-70	61	32
	Fall	-22.98	4.60	7 ± 6	0-28	17 ± 5	4-31	4 ± 4	0-18	6 ± 5	0-27			66 ± 2	61-70	58	25
GYF	Spring	-22.01	4.93	6 ± 5	0-23			6 ± 5	0-22			39 ± 5	27-51	48 ± 2	45-52	49	8
	Summer	-22.60	4.73	4 ± 4	0-19	28 ± 5	12-41	1 ± 1	0-8	5 ± 4	0-23			62 ± 1	59-65	55	14
	Fall	-22.66	3.96	10 ± 8	0-38	6 ± 4	0-20	7 ± 5	0-26	8 ± 6	0-30			70 ± 2	62-74	76	34

Table 5.7. Continued

		Signature		% Prey Composition												% Plant Estimate	
MALES	Season	δ13C	δ15N	Moose		Elk		Caribou		Sheep		Grazers		Plants		Hobson[1]	Literature[2]
				mean ± SD	range	mean ± SD	range	mean ± SD	range	mean ± SD	range	mean ± SD	range	mean ± SD	range		
AG	Spring	-22.36	4.35	5 ± 4	0-19			5 ± 4	0-18			19 ± 5	8-30	70 ± 2	67-73	65	20
	Summer	-22.45	4.32	11 ± 9	0-48	14 ± 8	0-41	4 ± 4	0-20	10 ± 8	0-37			60 ± 3	52-66	66	22
	Fall	-22.46	6.59	65 ± 4	58-73	28 ± 4	18-39	3 ± 3	0-10	5 ± 4	0-16			0		3	x
AM	Spring	-22.05	5.05	12 ± 8	0-36			11 ± 8	0-34			25 ± 6	9-41	52 ± 2	47-57	46	7
	Summer	-22.50	4.35	8 ± 7	0-40	20 ± 8	0-42	3 ± 3	0-14	9 ± 7	0-35			60 ± 2	54-65	65	21
	Fall	-22.46	5.30	4 ± 4	0-18	36 ± 4	27-47	3 ± 2	0-11	4 ± 3	0-17			54 ± 1	50-56	39	8
AO	Spring	-22.20	4.56	8 ± 6	0-26			8 ± 6	0-25			29 ± 5	15-43	56 ± 2	52-59	59	15
	Summer	-22.44	4.76	11 ± 9	0-48	16 ± 9	0-42	4 ± 4	0-19	10 ± 8	0-37			59 ± 2	52-65	54	12
	Fall	-22.28	5.28	4 ± 4	0-19	43 ± 4	34-54	3 ± 3	0-13	4 ± 4	0-17			46 ± 1	42-49	39	7
BQ	Spring	-22.27	5.08	14 ± 9	0-40			14 ± 9	0-40			21 ± 6	4-38	50 ± 3	44-56	45	11
	Summer	-22.62	4.53	9 ± 7	0-41	15 ± 8	0-37	3 ± 3	0-15	8 ± 7	0-31			65 ± 2	59-70	60	18
	Fall	-22.59	5.39	3 ± 3	0-13	48 ± 3	41-57	2 ± 2	0-9	3 ± 3	0-13			44 ± 1	42-46	36	9
BX	Spring	-22.10	3.91	8 ± 6	0-27			8 ± 6	0-27			14 ± 6	0-29	70 ± 2	65-74	77	26
	Summer	-22.46	5.18	13 ± 10	0-56	21 ± 10	0-52	5 ± 4	0-21	13 ± 10	0-46			49 ± 3	41-56	42	5
	Fall	-22.28	6.02	4 ± 3	0-16	60 ± 3	52-69	2 ± 2	0-10	3 ± 3	0-15			31 ± 1	28-34	19	0
BZ	Spring	-22.07	2.97											100		100	x
	Summer	-22.31	3.12											100		99	x
	Fall	-22.06	4.87	7 ± 6	0-29	22 ± 5	10-37	4 ± 4	0-19	6 ± 5	0-26			61 ± 2	55-64	51	12
CU	Spring	-23.21	3.82	8 ± 6	0-24			6 ± 5	0-19			6 ± 4	0-18	80 ± 2	76-84	80	46
	Summer	-23.20	3.05											100		100	x
	Fall	-22.94	4.39	6 ± 5	0-25	23 ± 4	12-37	3 ± 3	0-14	5 ± 4	0-22			63 ± 2	58-66	64	27
I	Spring	-22.20	3.90	5 ± 4	0-18			5 ± 4	0-17			19 ± 4	8-29	71 ± 1	68-74	77	29
	Summer	-22.44	4.17	13 ± 10	0-47	8 ± 6	0-33	8 ± 6	0-28	9 ± 7	0-34			63 ± 3	53-69	70	27
	Fall	-21.89	6.05	5 ± 5	0-24	57 ± 4	46-70	3 ± 3	0-15	5 ± 4	0-22			30 ± 2	25-33	18	0
Q	Spring	-21.86	4.37	6 ± 5	0-23			6 ± 5	0-22			27 ± 5	14-39	61 ± 2	57-64	65	4
	Summer	-22.31	2.92											100		100	x
	Fall	-22.24	4.90	10 ± 8	0-41	23 ± 5	7-38	6 ± 5	0-25	10 ± 7	0-38			51 ± 2	43-55	50	11
S	Spring	-22.85	4.04	6 ± 5	0-20			5 ± 4	0-20			12 ± 5	1-23	77 ± 2	74-80	74	32
	Summer	-22.95	5.02	8 ± 7	0-35	27 ± 8	0-48	3 ± 3	0-14	9 (0 - 38)	0-38	9 ± 7		54 ± 2	49-59	46	21
	Fall	-22.38	5.55	32 ± 4	27-40	65 ± 3	58-72	1 ± 1	0-4	2 ± 2	0-6			0		0	x
GKM	Spring	-23.10	5.76	8 ± 6	0-25			7 ± 6	0-25			47 ± 5	34-61	38 ± 2	34-42	26	x
	Summer	-23.32	4.62	13 ± 10	0-49	6 ± 5	0-28	12 ± 7	0-34	8 ± 7	0-35			61 ± 3	51-67	58	42
	Fall	-23.32	4.81	3 ± 3	0-14	28 ± 3	2-37	2 ± 2	0-9	3 ± 3	0-13			64 ± 1	61-66	52	x
GPM	Spring	-22.47	4.01	11 ± 8	0-35			10 ± 7	0-30			12 ± 6	0-28	66 ± 2	61-71	74	25
	Summer	-22.78	3.95	6 ± 6	0-29	15 ± 7	0-32	2 ± 2	0-11	7 ± 6	0-26			70 ± 2	66-74	76	31
	Fall	-22.46	4.71	6 ± 5	0-27	28 ± 5	16-42	4 ± 3	0-18	6 ± 5	0-25			56 ± 2	51-60	55	16

[1] Estimate generated using fractionation values as in Equation 2 in the text.
[2] Estimate generated from fractionation values ΔN = 3.0‰ and ΔC = 2.0‰, typically used in other diet determinations (e.g., Ben-David et al., 1997; Post, 2002).

Table D1. Continued

		N	Slope[b]	
			(%)	($\%^2$)
COY	**Spring**	928	0.07 ± 0.07	**-0.001 ± 0.0002**
Juveniles	**Summer**	378	0.02 ± 0.11	-0.0007 ± 0.02

			Prey Benefit			
			Moose	**Elk**	**Caribou**	**Sheep**
Juveniles	**Spring**	304	0.55 ± 0.53	**3.38 ± 0.91**	0.46 ± 0.56	**4.10 ± 0.70**

[a] Spring = den emergence - 15 June; Summer = 16 June - 15 August; Fall = 16 August - denning.
[b] Slope and elevation were entered in competing models as quadratic functions.
[c] No Aspect <1° slope.

Table D1. Habitat classes and their selection coefficients ($\beta_i \pm$ SE) from the best resource selection models by season for family groups of grizzly bears in the Besa-Prophet study area of northern British Columbia. Coefficients are based on pooled data between 2001 and 2004 (unless otherwise indicated). Values in bold indicate significant selection (positive values) or avoidance (negative values) as determined by 95 % confidence intervals.

Family Group	Season[a]	N	Conifer	Stunted Spruce	Shrub	Alpine Shrub	Non-Vegetated	Riparian	Open Alpine	Deciduous Burns	*Elymus* Burns	Sub-Alpine Spruce
COY	Spring	928	-0.30 ± 0.34	0.12 ± 0.41	-0.51 ± 0.53	0.16 ± 0.33	0.01 ± 0.35	0.54 ± 0.50	0.35 ± 0.33	-0.30 ± 0.39	'0.70 ± 0.37	-0.77± 0.42
	Summer	1659	-0.73 ± 0.29	-0.67 ± 0.38	0.24 ± 0.32	0.84 ± 0.28	-1.19 ± 0.36	-0.33 ± 0.40	-0.37 ± 0.33	0.82 ± 0.29	0.84 ± 0.33	0.54 ± 0.30
	Fall	1518	-0.65 ± 0.08	**-0.44 ± 0.12**	**0.48 ± 0.09**	**0.56 ± 0.09**	**-0.31 ± 0.11**	**0.25 ± 0.11**	**-0.67 ± 0.16**	**0.22 ± 0.09**	**0.54 ± 0.10**	0.03 ± 0.11
Yearlings	Spring	1159	**-0.56 ± 0.09**	0.19 ± 0.15	**-0.71 ± 0.16**	**-0.28 ± 0.10**	**0.45 ± 0.10**	0.26 ± 0.17	-0.03 ± 0.11	**0.34 ± 0.10**	**0.75 ± 0.12**	**-0.40 ± 0.13**
	Summer	1390	**-0.73 ± 0.09**	**-0.49 ± 0.13**	**0.48 ± 0.12**	**0.76 ± 0.07**	**-1.62 ± 0.13**	0.20 ± 0.14	**-0.67 ± 0.10**	**0.92 ± 0.09**	**0.86 ± 0.12**	**0.31 ± 0.10**
	Fall	1133	**-0.71 ± 0.09**	-0.17 ± 0.12	**0.51 ± 0.10**	0.17 ± 0.12	-0.21 ± 0.13	0.21 ± 0.12	**-0.69 ± 0.18**	**0.23 ± 0.11**	**0.44 ± 0.13**	0.21 ± 0.12
Juveniles	Summer	378	-0.56 ± 0.37	-0.03 ± 0.46	0.27 ± 0.44	0.36 ± 0.37	-0.94 ± 0.48	0.47 ± 0.43	-0.77 ± 0.45	0.25 ± 0.44	0.43 ± 0.49	0.52 ± 0.41
	Fall	447	-0.53 ± 0.65	-0.01 ± 0.74	-0.22 ± 0.78	0.02 ± 0.80	-0.58 ± 0.92	-0.49 ± 0.81	0.07 ± 0.91	0.30 ± 0.75	1.26 ± 0.79	0.18 ± 0.78
Alone	Spring	621	-0.42 ± 0.34	0.52 ± 0.39	-0.41 ± 0.44	0.01 ± 0.37	-0.50 ± 0.43	-0.006 ± 0.48	-0.07 ± 0.41	0.42 ± 0.38	0.70 ± 0.43	-0.25 ± 0.42
	Summer	1347	**-0.43 ± 0.08**	**-0.34 ± 0.13**	-0.05 ± 0.11	**1.06 ± 0.09**	**-1.08 ± 0.16**	0.14 ± 0.14	**-0.41 ± 0.13**	**0.55 ± 0.11**	0.08 ± 0.17	**0.50 ± 0.11**
	Fall	1512	-0.30 ± 0.26	-0.20 ± 0.35	0.37 ± 0.31	-0.04 ± 0.34	-0.67 ± 0.36	-0.06 ± 0.35	-0.42 ± 0.38	0.17 ± 0.32	1.02 ± 0.33	0.14 ± 0.34

		N	Elevation[b]	Fragmentation				Aspect[c]				
			(km)	(km^2)	Low	Medium	High	North	East	South	West	No Aspect
COY	Spring	928	**17.55 ± 4.20**	**-5.29 ± 1.37**	-0.53 ± 0.28	0.02 ± 0.25	**0.51 ± 0.24**	-0.36 ± 0.40	0.20 ± 0.38	0.37 ± 0.38	0.01 ± 0.39	-0.21 ± 0.72
	Summer	1659	**11.36 ± 1.24**	**-3.59 ± 0.70**	-0.10 ± 0.18	0.03 ± 0.17	0.07 ± 0.17	0.22 ± 0.25	-0.20 ± 0.25	-0.35 ± 0.25	-0.07 ± 0.27	0.41 ± 0.38
	Fall	1518	**13.85 ± 1.58**	**-5.27 ± 0.53**	**-0.15 ± 0.05**	0.02 ± 0.04	**0.13 ± 0.04**	0.04 ± 0.07	-0.08 ± 0.07	**0.27 ± 0.06**	**0.17 ± 0.07**	**-0.41 ± 0.17**
Yearlings	Spring	1159	**21.03 ± 1.99**	**-6.76 ± 0.63**	**-0.17 ±0.06**	-0.01 ± 0.05	**0.18 ± 0.05**	**-0.31 ± 0.10**	**0.18 ± 0.09**	**0.55 ± 0.09**	-0.12 ± 0.11	-0.30 ± 0.30
	Summer	1390	**0.05 ± 0.01**	**-0.001 ± 0.0001**	**-0.19 ±0.05**	0.001 ± 0.05	**0.19 ± 0.05**	**0.33 ± 0.07**	**-0.36 ± 0.07**	**-0.19 ± 0.07**	-0.08 ± 0.08	0.31 ± 0.18
	Fall	1133	**14.42 ± 1.90**	**-5.57 ± 0.66**	**-0.18 ± 0.06**	-0.04 ± 0.05	**0.21 ± 0.05**	0.03 ± 0.08	**-0.37 ± 0.07**	-0.01 ± 0.07	**0.20 ± 0.08**	0.15 ± 0.15
Juveniles	Summer	378	-0.02 ± 0.07	0.005 ± 0.04	-0.22 ± 0.30	0.03 ± 0.26	0.19 ± 0.26	0.01 ± 0.06	0.007 ± 0.06	-0.03 ± 0.07	0.008 ± 0.07	0.006 ± 0.09
	Fall	447	**14.71 ± 3.58**	**-5.89 ± 2.13**	0.005 ± 0.07	-0.004 ± 0.06	-0.0008 ± 0.06	-0.07 ± 0.55	0.03 ± 0.55	-0.29 ± 0.56	0.18 ± 0.57	0.15 ± 0.82
Alone	Spring	621	**18.72 ± 1.73**	**-5.91 ± 0.98**	-0.30 ± 0.30	-0.006 ± 0.26	0.31 ± 0.26	-0.03 ± 0.06	-0.01 ± 0.05	0.007 ± 0.05	0.004 ± 0.05	0.03 ± 0.09
	Summer	1347	**3.54 ± 1.40**	**-1.44 ± 0.43**	**-0.20 ± 0.06**	0.03 ± 0.05	**0.16 ± 0.05**	**0.32 ± 0.07**	**-0.21 ± 0.07**	**-0.24 ± 0.07**	-0.15 ± 0.08	0.28 ± 0.15
	Fall	1512	**15.98 ± 1.42**	**-5.87 ± 0.83**	-0.007 ± 0.06	-0.007 ± 0.06	0.01 ± 0.06	0.16 ± 0.26	-0.03 ± 0.26	0.07 ± 0.25	-0.44 ± 0.29	0.24 ± 0.39